1-1-2004

Scarce resources and party size in a community of savanna chimpanzees in southeastern Senegal

Alexander Kenneth Piel
Iowa State University

Scarce resources and party size in a community of savanna chimpanzees in southeastern Sénégal

by

Alexander Kenneth Piel

A thesis submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

MASTER OF ARTS

Major: Anthropology

Program of Study Committee:
Jill D. Pruetz, Major Professor
Anne Bronikowski
Hsain Ilahiane
Rolf Koford

Iowa State University

Ames, Iowa

2004

Graduate College
Iowa State University

This is to certify that the master's thesis of

Alexander Kenneth Piel

has met the thesis requirements of Iowa State University

Signatures have been redacted for privacy

To my greatest mentor, and closest friend -

DKC

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGEMENTS

This thesis would not have been possible without tremendous intellectual, financial, and emotional support from many people. First and foremost, without the generous permission granted to Jill Pruetz and her students to live and work in Kédougou by the government of Sénégal, specifically Eaux et Foret, Departement du Kédougou, région de Tomboronkoto, you wouldn't have anything to read right now. I hope that along with all the other products that stem from this project, Sénégal will grow to appreciate and value the few chimpanzees that remain there. My project was, in part, funded by a Liberal Arts & Sciences Faculty Development Grant awarded to JDP by Iowa State University. Without this logistical and financial support, this project could not have happened. I am likewise indebted to the local people of Fongoli and its neighboring villages who have grown to appreciate and protect their knuckle-walking neighbors with whom they share the land. Many thanks to the research assistants and field guides who come from these areas and tolerated my relentless pursuit of the savanna chimpanzee. Surtout j'ai besoin de remercier CAMARA Mboule and KANTE Dondo pour leur travail et leur loyauté sur cette projet. Vous êtes toujours plus forts que moi.

A squad of colleagues, friends, and professors have helped me develop and organize many of the ideas herein. For his assistance and mastery of Statistics I thank *Reid Landes* of Iowa State University. He simultaneously taught and helped me conduct the tests that follow, never impatient with my unrelenting nagging! In the Interlibrary Loan Office at Iowa State University, *Wayne Pedersen* was able to locate and retrieve obscure and buried sources time and time again. There is a not a single article, dissertation, or book that his office couldn't and didn't locate promptly over the course of my research: many thanks to him for all his efforts. I thank *Rolf Koford* for reading, re-reading and re-re-reading drafts of this work since the proposal was under initial construction in 2002. He has contributed insightful suggestions and editorial improvements, significantly enhancing the quality of this thesis. More importantly, he encouraged me to address questions I would have otherwise neglected and I am grateful for his enduring patience and interest in the work. Special thanks also to *Anne*

Bronikowski and *Brian Smith* for their reading of specific chapters. Thanks also to *my family* who has accepted and embraced this journey I have begun and the path I continue to create and follow. To *Fiona Stewart*, who, unknowingly, inspires me personally and professionally. You are a part of this work in so many ways. More than anyone, *Jill Pruetz* has shown extraordinary flexibility and availability throughout my career in Ames. She has put up with me from class to Kédougou, all the while providing incessant enthusiasm and, without hesitation, confidence in my abilities to complete this MA. For her unconditional support I am ever grateful. Without such a network of support from everyone mentioned here and many others, I could not have completed this.

Finally, I would be remiss if I failed to acknowledge the threat that all wild chimpanzees, savanna and forested, face today. Depressingly and regrettably, our time with such extraordinary creatures dwindles with each day as we realize more and more how blessed we are to share in their lives and in their worlds. Let us not refrain from taking all necessary steps to protect what critical ape habitats and wild populations remain on this planet.

ABSTRACT

Current paleo-environmental data suggest early hominins evolved in mosaic habitats of wooded grasslands and open savannas. With numerous pressures acting on physiological, morphological, and behavioral changes, these hominins are presumed to have undergone profound evolution in order to adapt to such extreme and sudden change in their surroundings. With the fossil record providing clues into this climatic and anatomical evolution, some of the foremost questions that remain in this search for identity and history concern the evolution of behavior, particularly primate sociality. Populations of savanna chimpanzees are long thought reliable referential models for many of these questions considering the similar nature of their environmental conditions to those of early *Australopithecus* and *Homo*.

The current study sought to do just that, hypothesizing that chimpanzees living in extreme ecological conditions will adapt their daily and nightly grouping behavior to, not the availability, but the *distribution* of critical food (and water) resources. Implications for such behavior may shed light on how human ancestors themselves responded to dramatic ecological change. All known feeding trees were located and densities for six of them were found within a 63 km^2 area thought to be the core range for the Fongoli community, southeast Sénégal. Observations were made on daily chimpanzee and nest grouping patterns for comparisons with forested and savanna communities in East and West Africa. In doing so, the ambiguity and diversity of 'party' definition was explored, with emphasis on how the chosen definition affects reported data.

Results from the study do, in fact, suggest that this population of chimpanzees forms smaller day parties as feeding trees and water sources become more widely dispersed. Moreover, comparisons of mean nest group sizes to daily ones indicate that perhaps to compensate for reduced interaction during the day, these chimpanzees aggregate in larger parties at night in an effort to maintain the strong social bonds that characterize the species. This behavior is already thought to exist in other savanna populations and would support earlier claims of specific savanna chimpanzee adaptations. Grouping behavior of this sort,

however, would contradict earlier suggestions that nesting behavior is a direct reflection of the social dynamics within a particular community of apes. Instead, I propose that daily and nesting behavior in these chimpanzees are acutely sensitive to and are an accurate reflection of the extreme ecological conditions of an open, dry, savanna habitat.

Chapter One: Introduction

"It is the versatility that chimpanzees show which enables them to survive in such an environment, and this versatility may be another manifestation of the same quality that reveals itself in their flexible social organization and comparatively high intellectual capacity."

P Baldwin, WC McGrew, CEG Tutin, 1982

1.1 Why study savanna chimpanzees?

Chimpanzees *(Pan troglodytes)* can be found across equatorial Africa (McGrew, 1992; Wrangham, 1994) (Figure 1.1.), with most populations existing within or near tropical moist forests and so not thought to be threatened with extreme seasonal pressures of famine or drought. These populations have been the most studied. Populations, however, that exist in Mali (Baffing: Duvall, 2000, 2001), western Uganda (Semliki: Hunt et al., 1999; Hunt and McGrew, 2002), western Tanzania (Filabanga: Suzuki, 1969; Kano, 1971, 1972; Ugalla: Hernandez, unpub data; Moore, 1992), and southeastern Sénégal (Assirik: McGrew et al., 1981; Baldwin et al., 1982, Tutin et al., 1983; Fongoli: Pruetz, 2002, Pruetz et al., 2002; current study) do face conditions significantly more unfavorable. Because it is in these latter ecologically challenging conditions that many think early *Homo* may have evolved (Reed, 1997), anthropologists have often used savanna chimpanzees as referential models to better understand mechanisms and patterns of adaptation (Potts, 1987; Tanner, 1987; Moore, 1996).

Studying savanna chimpanzee ecology allows researches to ask questions not possible with forest dwelling ones. For example, although much behavioral variation between chimpanzee populations is ultimately caused by ecological differences, some is thought to be culturally induced, with variation found across a diverse array of behaviors (Whiten et al., 1999). Understanding the significance of these differences and how they originated can shed important light on the processes acting on the evolution of culture (Bonner, 1980; McGrew, 1992). One question, then, we can ask is to what extent culture and ecology each contribute to observed behavior. Examining savanna chimpanzees allows ecology to be a more salient

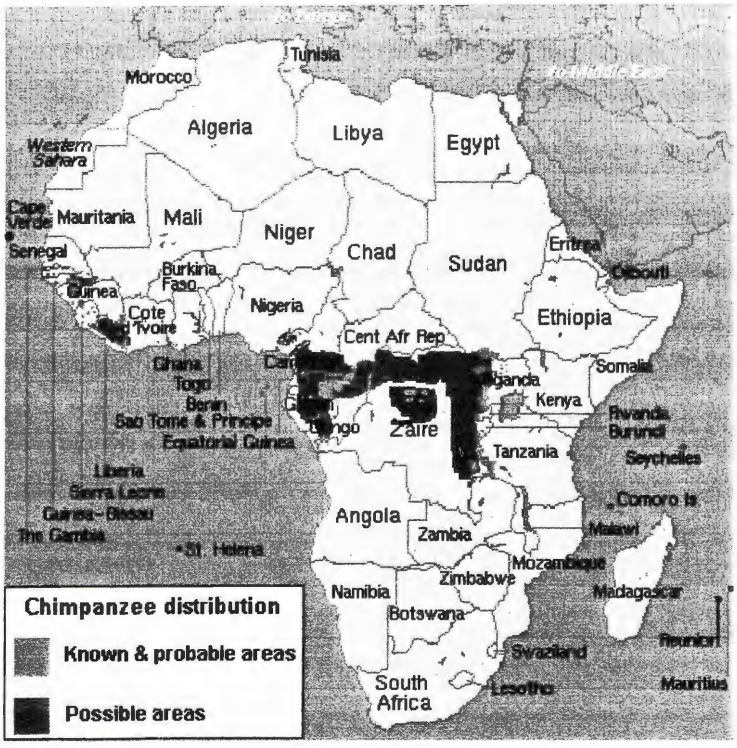


Fig. 1.1. Chimpanzee distribution across Africa

part of this question. Second, with recent evidence of climatic instability and habitat variability from the early Plio-Pleistocene (Reed, 1997; Wynn, 2004) supporting the hypothesis that hominins evolved in savanna mosaics (Dart, 1925), investigations into chimpanzee ecological and social adaptations to a similar habitat (such as Fongoli, Baffing, Semliki, and Ugalla may offer – see Figure 1.2.), complemented by observations of extant hunter-forager groups (Yellen, 1976), may provide insight into behaviors not reflected in the fossil record (i.e. social grouping patterns, shifts in ranging, diet, etc). For this reason and for their significance in modeling how early hominins may have adapted to sudden and drastic changes in ecology (Moore, 1992, 1996; Reed, 1997), savanna chimpanzees represent important pieces to our overall understanding of primate, and specifically ape, socioecology.

Finally, it is thought that the chimpanzee fission-fusion social system has evolved as a strategy to reduce intra-group feeding competition for patchy and ephemeral large fruits (Wrangham, 1986; Newton-Fisher et al., 2000). In most areas, savanna chimpanzees already face high competition from increasing human populations for available food sources during

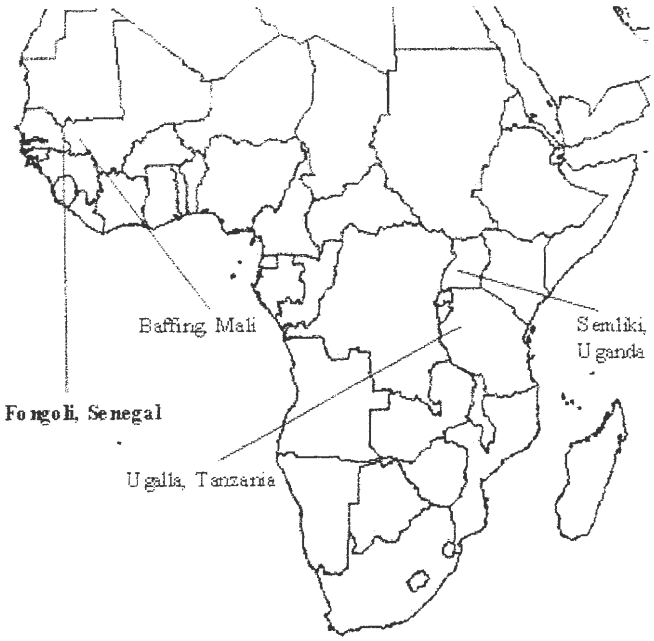


Fig. 1.2. Current savanna chimpanzee study sites

the late dry season (Duvall, 2000; Pruetz, 2002). High quality fruit sources, on which chimpanzees rely for most of their diet (Matsumoto-Oda and Hayashi, 1999; Tweheyo and Lye, 2004), may be found at very low densities in these savanna regions, typically characterized by lower flora diversity than tropical areas (Bouliere and Hadley, 1970). Expanding agricultural practices in some areas may infringe on critical travel routes used by chimpanzees (see Chapter Two; Moore, 1992), as well as eradicate their food sources. When this competition is combined with extreme seasonality and the potential for famine and drought for either species, chimpanzee survival in these marginal areas is uncertain (Kortlandt, 1983). How chimpanzees modify their social organization in response to such conditions is critical to our understanding of their behavioral flexibility and will be a central focus of the current study.

1.2 The Problem

The evolution of sociality in animals has long been at the forefront of mammalian behavioral research (Eisenberg and Kleinman, 1983; Rubenstein and Wrangham, 1986; Janson, 2000; Kappeler and van Schaik, 2002). Efforts to assess and understand the direct

and indirect influences of grouping patterns, however, have focused on the costs and benefits animals must balance when forming groups, especially in those species that can easily manipulate the size of their group (Chapman et al., 1995; Chapman and Chapman, 2000). Although most primates live socially and forage and travel in unit-groups (Chapman and Chapman, 2000), few species exhibit the fluidity and flexibility of chimpanzees. We now know that chimpanzee sociality works on two levels: (1) a community or group of male-bonded individuals who are socially tolerant, but who (2) interact and move in parties or sub-groups (Nishida, 1968; Goodall, 1986; Chapman et al., 1993). Initially labeled as woodland nomads (Suzuki, 1969), chimpanzees were thought to aggregate seasonally with individuals joining and departing randomly and freely. Association patterns (e.g. fissioning and fusioning) in well known communities are now thought to respond to particular alliances (Newton-Fisher, 1999), predation risks (Tutin et al., 1983; Boesch, 1991), hunting opportunities (Boesch & Boesch, 1989; Mitani and Watts, 1999; Anderson et al., 2002), activities and proximity to core areas (Anderson et al., 2002), and mating opportunities (Goodall, 1986). Moreover, females have been seen to be coerced and violently forced into consortships with dominant males.

In poorer known savanna communities, however, chimpanzees may be adopting atypical behaviors to cope with such extreme ecological conditions. Moore (1992) suggested that these "savanna adaptations" may be the result of the inefficiency of normal fission-fusion systems to operate in such areas. Hernandez (pers. comm.), after spending two years in Ugalla, western Tanzania, observed large numbers of clumped nesting parties. This "spatial redundancy" (Sept, 1998) may be a reflection of (a) limited trees in which chimpanzees can nest, (b) actual preferred areas, or (c) a means of compensating for lost time together during the day. If scarce resources demand increased travel and consequently, the formation of smaller daily parties, aggregating at night in large nest groups may allow individuals within a community to maintain social cohesion.

A second issue to be addressed in the current study is how various interpretations of chimpanzee temporary groupings may influence our understanding of their social system. More than fifteen different definitions of 'party' have been used in studies of wild chimpanzees (Table 1.1), most which vary considerably (Chapman et al., 1993). Addressing

this inconsistency is critical if we hope to understand the ultimate causes of behavioral variation in chimpanzees (McGrew, 1992; Whitten et al., 1999).

1.3 The Approach

Objectives

Individuals are hypothesized to aggregate in party sizes that allow for optimum exploitation of resources (Wrangham et al., 1993; Newton-Fisher et al., 2000). This study used daily observational and nest-count data to estimate party size and investigate the effect scarce resources had on chimpanzee grouping behavior. Seasonal waterholes and feeding-tree preferences as well as chimpanzee vocalizations were used to locate groups and data collected on both daily and nesting party size at Fongoli were compared to those found at other sites where chimpanzees have been studied. Furthermore, specific attention was paid to how previous studies have defined chimpanzee 'party' and how different definitions may influence the reported findings and subsequent comparisons. The objectives of this study, then, were to examine

1. *daily party size and composition as determined by behavioral observation,*
2. *sleeping party size, determined by the occurrence of fresh chimpanzee nests, and*
3. *how our understanding of chimpanzee 'parties' varies across sites*

Comparisons across sites

Comparing mean group size estimates across sites can be problematic, even when definitions are standardized (which remains to be done for chimpanzees) (MacDonald et al., 2000). First, it is often difficult to count individuals that are dispersed throughout a habitat where visibility is limited, such as in dense forest patches. The greater the distance between the focal group and observer, the higher the probability that an animal will be neglected in a final count. Other contributing variables include the level of habituation of the target community (although see Morgan & Sanz, 2003) and the duration of the study (Chapman et al., 1993). Finally, Chapman et al. (1993) suggest that the method of detecting parties will significantly influence resulting data. For example, in Kibale National Park, Uganda,

TABLE 1.1. Different 'party' definitions

"Party" Definition	Source
# of individuals that move together by remaining in visual and vocal communication with each other (when distance <200m)	Sugiyama & Koman, 1979
As the focal animal and all others within 100m	Wrangham & Smuts, 1980
# of individuals present at the beginning of an observation period	Tutin et al., 1983; White, 1988*; Fruth, 1995^; Pepper et al., 1999; Mitani et al., 2002
# of individuals that move together by remaining in visual contact of each other	Boesch, 1991*
# of individuals in a single scanning sample	Wrangham et al., 1992
# of individuals within a 30m radius	Sakura, 1994^
Subgrouping of individuals from one community at a specific time and place	Fruth, 1995^
# of individuals in sight of one another; in auditory contact; within a certain distance	Boesch, 1996*#
# of adults and adolescents present in a given hour	Chapman et al., 1994^; Doran, 1997^
# of individuals interacting each day while following the focal chimpanzees	Matsumota-Oda et al., 1998
# of individuals present each day	Sakura, 1994; Boesch, 1996*#; Matsumota-Oda, 1999
Collection of independently associating individuals showing coordination in behavior; cluster of individuals with a radius around 35m	Newton-Fisher, 1999
Largest number of individuals observed in one place (all individuals seen or known to be present by observer)	Newton-Fisher et al., 2000
Group including adults and subadults	Lanjouw, 2002^

* indicates party count updated upon any change in composition # indicates definition varied with observer

^ indicates juveniles and infants were NOT included in party count

Wrangham et al. (1992) found that parties found using chimpanzee vocalizations were larger (5.1) than those found at fruiting trees (2.4). Likewise, "acoustic" subgroups (mean party size = 7.1) differed significantly from overall subgroups (mean party size = 5.11) in a similar study at the same site (Chapman et al., 1993). These differences can be problematic because variation in reported mean party sizes may reflect discrepancies in methodologies rather than actual differences among communities. Thorough descriptions of habitats are necessary when comparing results across sites, especially if we wish to examine the exact nature of the

influences on behavioral variation. In the current study, party size was examined in response to social, ecological, and methodological variables.

1.4 Hypotheses

The proposed research is important anthropologically as it allows for the testing of hypotheses (see Wrangham, 1980; Wrangham et al., 1993, 1998; Gillespie & Chapman, 2001) aimed at understanding how food distribution and habitat type affect the social organization of group-living primates. Likewise, it exposes the need for researchers to standardize definitions. Despite extermination of most predators, chimpanzees here still face competition with humans from the Bassari, Bédik, Diahanké, and Malinké tribes for scarce food and water sources (Pruetz, 2002; Knutsen, 2003). Moreover, with a rapidly increasing human population in the immediate area - 91% since 1976 (Sall, 2000) – the neighboring groups of apes may have to modify their social and ecological behaviors to accommodate this influx: less abundant and more dispersed food sources should force chimpanzees to form smaller parties to forage more efficiently for adequate sustenance (Boesch, 1991; Chapman et al., 1995; Matsumoto et al., 1998). This will be reflected in both daily and nest party sizes. Thus, it is hypothesized that

1. *Savanna chimpanzees form smaller parties than forest chimpanzees in response to a more dispersed and scarce food supply*
2. *H_o: Mean nest party size will not be different from mean daily party size*
3. *Different definitions of 'party' will yield different mean party sizes*

1.5 Conservation Implications

Originally estimated at 600,000 individuals in 1989 (Teleki, 1989), Western chimpanzees *(P. t. verus)* now number between 25,000-52,000 and are considered endangered by the Union for Conservation of Nature and Natural Resources (Table 1.2; Kormos et al., 2003). Initially found throughout western Africa, these apes have already been exterminated in three countries (Benin, The Gambia and Togo) with four more hosting

only small and isolated communities: Burkina Faso, Ghana, Guinea Bissau, & Sénégal (Butynski, 2003). A 2002 conference in Ivory Coast named the Mandingue Plateau (which includes SE Sénégal) as one of seven sites critical to the conservation of West African chimpanzees (Kormos et al., 2003). Despite a history of coexistence between humans and chimpanzees in this region, recent human population increases are threatening this co-existence (Duvall, 2000; Sall, 2000; Pruetz, 2002;). Because it is hypothesized that chimpanzee social grouping is a direct reflection of the quality of their habitat,

Table 1.2. Distribution of all 4 subspecies of chimpanzee, Pan troglodytes (from Butynski, 2003)

Sub-species	# Remaining	Range (km^2)
Robust Chimpanzee *(Pan troglodytes)*	200,000	838,000
Western Chimpanzee *(P.t. verus)*	40,000	48,000
Nigerian Chimpanzee *(P.t. vellerosus)*	5,000	20,000
Central Chimpanzee *(P.t. troglodytes)*	62,000	270,000
Eastern Chimpanzee *(P.t. schweinfurthii)*	96,000	500,000

examining party size in the Fongoli community is crucial to further our understanding of how human expansion and habitat alteration affect chimpanzee behavioral ecology. Combined with data currently being collected on food abundance as part of a long term study on the socioecology of chimpanzees in this region, the results of this project will allow us to more comprehensively explore solutions to promoting the continued coexistence of these two primate species in the region.

Sources

Anderson DP, Nordheim EP, Boesch C, Moermond TC. 2002. Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 90-101.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *International J of Primatol* 3(4):367-385.

Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies.* Cambridge: Cambridge University Press. p 101-113.

Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117:220-242.

Boesch CA, Boesch-Achermann H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Amer J of Phys Anthropol* 78:547-573.

Bonner JT. 1980. *The Evolution of Culture*. New Jersey: Princeton University Press.

Bouliere F, Hadley M. 1970. The ecology of tropical savannas. *Ann Review of Ecology and Systematics* 1:125-152.

Butynski TM. 2003. The robust chimpanzee *Pan troglodytes:* Taxonomy, Distribution, Abundance and Conservation Status. In: Kormos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan.* Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p 5-12.

Carter J, Ndiaye S, Pruetz J, McGrew WC. 2003. Senegal. In: Kormos R, Boesch C, Bakarr MI, Butynski TM, editors, *West African Chimpanzees: Status Survey and Conservation Plan.* Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources. p 31-40.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: The importance of travel costs. In: Boinski S, Garber PA, editors, *On the move: How and why animals travel in groups,* Chicago and London: University of Chicago Press. p 24-42.

Chapman CA, Wrangham RW, Chapman CA. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiology* 36:59-70.

Chapman CA, White FJ, Wrangham RW. 1994. Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors, *Chimpanzee Cultures*, Cambridge: Harvard University Press. p 41-58.

Chapman CA, White FJ, Wrangham RW. 1993. Defining subgroup size in fission-fusion societies. *Folia Primatol* 61:31-34.

Dart R. 1925. *Autraliapithecus africanus,* the man-ape of South Africa. *Nature* 115:195-199.

Doran D. 1997. Influence of Seasonality on activity patterns, feeding behavior, ranging and grouping patterns in Tai chimpanzees. *Int'l J of Primatol* 18(2):183-206.

Duvall CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21(4):173-203.

Duvall CS. 2001. Habitat, conservation, and use of *Gilletiodendron glandulosum* (Fabacae, Caesalpinoideae) in southwestern Mali. *Sys. Geogr* 71:699-737.

Eisenberg JF, Kleiman DG, editors. 1983. Advances in the study of mammalian behavior. Shippensburg, PA: American Society of Mammalogists.

Fruth B. 1995. Nests and nest groups in wild bonobos *(Pan paniscus)*: Ecological and behavioural correlates. Aachen: Verlag Shaker.

Gillespie TR, Chapman CA. 2001. Determinants of group size in the red colobus monkey *(Procolobus badius)*: an evaluation of the generality of the ecological-constraints model. *Behav Ecol Sociobiol* 50(4):329-338.

Goodall, J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: The Belknap Press of Harvard University,.

Hunt KD, Cleminson AL, Latham J, Weiss RI, Grimmond S. 1999. A partly habituated community of dry habitat chimpanzees in the Semliki Valley Wildlife Reserve, Uganda. *Amer J of Phys Anthropo,* Supply. 28, 157.

Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Mont Assirik, Sénégal and Semliki Wildlife Reserve, Uganda. In: McGrew WC, Marchant L, Nishida T, editors, Great Ape Societies. Cambridge: Cambridge University Press. p 35-51.

Janson, CH. 2000. Primate socio-ecology: The end of a golden age. *Evol Anthropol* 9(2):73-86.

Kappeler, PM. van Schaik CP. 2002. Evolution of primate social systems. *International J of Primatol* 23(4):707-740.

Kortlandt A. 1983. Marginal habitats of chimpanzees. *J of Human Evolution* 12:231-278.

Kormos R, Boesch C, Bakarr MI, Butynski TM. Editors. 2003. *West African Chimpanzees: Status Survey and Conservation Plan.* Gland, Switzerland and Cambridge, UK: Union for Conservation of Nature and Natural Resources.

Lanjouw A. 2002. Behavioural adaptations to water scarcity in Tongo chimpanzees In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 52-60.

MacDonald DM., Stewart PD, Stopka P, Yamaguchi N. 2000. Measuring the dynamics of mammlian societies: an ecologists guide to ethological methods. In: Boitani L, Fuller K, editors, *Research Techniques in Animal Ecology: Controversies and Consequences,* New York: Columbia University Press.

Matsumoto-Oda A. 1999. Mahale Chimpanzees: Grouping patterns and cycling females. *Amer J of Primat* 47:197-207.

Matsumoto-Oda A, Hayashi Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatol* 70(3):154-162.

Matsumoto-Oda A, Osaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *Int'l J of Primatol* 19(6):999-1011.

McGrew WC. 1992. *Chimpanzee Material Culture*. Cambridge: Cambridge University Press:

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirk, Sénégal, West Africa. *J of Human Evolution* 10:227-244.

Mitani JC, Watts DP. 1999 Demographic influences on the hunting behavior of chimpanzees. *American J of Phys Anthropol* 109(4):439-454.

Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol* 11(1):9-25.

Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies.* Cambridge: Cambridge University Press. p 275-292.

Moore J. 1992. 'Savanna chimpanzees'. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 99-118.

Morgan D, Sanz C. 2003. Naive encounters with chimpanzees in the Goualougo Triangle, Republic of Congo. *International J of Primatol* 24(2):369-381.

Newton-Fisher NE. 1999. Association by male chimpanzees: A social tactic. *Behaviour* 136:705-730.

Newton-Fisher NE, Reynolds V, Plumptre AJ. 2000. Food supply and chimpanzee *(Pan troglodytes schweinfurthii)* party size in the Budongo Forest Reserve, Uganda. *International J of Primato* 21(4):613-628.

Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.

Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International J of Primatol* 20(5):613-632.

Potts R. 1987. Transportation of resources: Reconstructions of early hominid socioecology: a critique of primate models. In: Kinsey W, editor, *The evolution of human behavior: Primate models,* Albany: State University of New York Press. p 28-50.

Pruetz JD. 2002. Competition between savanna chimpanzees and humans in southeastern Sénégal. *Amer J Phys Anthropol* 128-128 Suppl. 34 2002.

Pruetz JD, Marchant LF, Arno J, McGrew WC. 2002. Survey of chimpanzees *(Pan troglodytes verus)* in southeastern Sénégal. *American J of Primatol* 58:35-43.

Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J of Human Evolution* 32(2-3):289-322.

Rubenstein DI, Wrangham RW, editors, 1986. *Ecological Aspects of Social Evolution: birds and mammals.* Princeton, New Jersey: University Press.

Sakura O. 1994. Factors affecting party size and composition of Chimpanzees *(Pan troglodytes verus)* at Bossou, Guinea. *International Journal of Primatology* 15(2):167-183.

Sall M. 2000. *Atlas du Senegal.* Paris: Les Editions J.A.

Sugiyama Y, J. Koman. 1979. Social structure and dynamics of Wild chimpanzees at Bossou, Guinea. *Primates* 20(3):323-339.

Suzuki A. 1969. An ecological study of chimpanzees in a savanna woodland. *Primates* 10:103-148.

Tanner NM. 1987. Gathering by females: the chimpanzee model revisited and the gathering hypothesis. In: Kinsey E, editor, *The Evolution of Human Behavior: Primate models,* Albany: State University of New York. P 3-28

Teleki G. 1989. Population status of wild chimpanzees *(Pan troglodytes)* and threats to survival. In: Heltne PG, Marquardt LA, editors, *Understanding Chimpanzees*, Cambridge, Massachusetts: Harvard University Press. p 312-353.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

Tweheyo M, Lye KA, Weladji RB. 2004. Chimpanzee diet and habitat selection in the Budongo Forest Reserve, Uganda. *Forest Ecol Manag* 188(1-3):267-278.

White FJ. 1988. Party composition and dynamics in *Pan paniscus*. *Int'l J of Primatol* 9(3):179-193.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch, C. 1999. Cultures in chimpanzees. *Nature* 399 (6737):682-685.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham RW. 1986. Ecology and relationships in two species of chimpanzee. In: Rubenstein DI, Wrangham RW, editors, *Ecology and Social Evolution: Birds and Mammals,* Princeton, New Jersey: Princeton University Press. p 353-378.

Wrangham RW. 1994. Overview – Ecology, Diversity, and Culture In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors, *Chimpanzee Cultures*, Cambridge: Harvard University Press. p 21-24.

Wrangham RW, Conkilin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int J of Primatol* 19(6):949-970.

Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: Population density and day-range assays of exploitation competition. *Behav Ecol Sociobiol* 32:199-209.

Wrangham RW, Clark AP, Isabirye-Basuta G. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 81-98.

Wrangham RW, Smuts BB. 1980. Six differences in the behavioural ecology of chimpanzees in the Gombe Stream National Park, Tanzania. *J Reprod Fert* 28:13-31.

Wynn JG. 2004. Influence of Plio-Pleistocene aridification on human evolution: Evidence from paleosols of the Turkana Basin, Kenya. *Amer J Phys Anthropol* 123(2):106-118.

Yellen JR. 1976. Settlement patterns of the !Kung: An Archaeological Perspective. In: Lee RB, Devore I, editors, *Kalahari Hunter-Gatherers: Studies of the !Kung San and Their Neighbors*, Cambridge: Harvard University Press. p 47-72.

Chapter Two: Primate Sociality

2.1 Introduction: Modeling

Examining the ecological determinants of social grouping has long been a central focus in the study of mammalian social behavior (antelope: Jarman, 1974; badgers: Krukk, 1989; bats: Bradbury and Vehrencamp, 1976; birds: Waser and Sahvi, 1973; hyenas: Holecamp et al., 1997; lemurs: Sussman, 1977; lions: Schaller, 1972; Sponge et al., 2002; rodents: Lee, 2004; primates (general): Wrangham, 1980; Treves and Chapman, 1996; Lefebvre et al., 2003; whales: Ottensmeyer & Whitehead, 2003; wild dogs: Frame et al., 1979). Unlike most mammalian taxa, in which gregariousness is atypical, social groups are characteristic of the Order Primates. Conceptual and quantitative models (see below) of sociality have proven useful for better understanding how ecological and social factors combine to affect group dynamics. However, because social organization is defined as "a heterogeneous set of spacing and social behaviors that characterize a population of animals of known age and sex" (Richards, 1985:292), most studies must use indirect measures or create models to predict behavior (see below).

Single-factor Model

Early models of primate sociality emphasized the distribution of food sources. Large, high quality food patches were thought to provoke female-bonded (FB) groups. Such groups would subsequently demonstrate high levels of intergroup competition. The most influential of these models provided an impetus for much research in the years following its publication, predicting that larger FB social groups would outcompete smaller ones and monopolize higher quality food resources (Wrangham, 1980). Tree-fruits, an example of a high quality food resource, are typically scattered in isolated patches, either individually or in small groups. As a result, single patches are normally insufficient to meet the energy requirements of social groups. The density and distribution of these resources, Wrangham (1980) hypothesized, were critical in the evolution of group living in primates. He suggested that when high quality foods were clumped, females should be philopatric, exhibiting strong

intergroup aggression to defend such resources. He went on to predict what ecological conditions would prompt female "differentiated relationships" and strong or weak female bonds. Wrangham et al. (1992) tested these predictions in chimpanzees and other group living primates, examining the behavioral consequences of social adaptations to ecology. These early FB-models revolutionized how researchers studied primates in the wild.

Multiple-factor Models

Wrangham's (1980) model, however, was unable to explain why non-FB primate species also live in groups [e.g. hamadryas baboons *(Papio hamadryas),* red colobus *(Colobus badius),* gorillas *(Gorilla gorilla)]*. In their attempt to integrate these and other species and to "incorporate more complex combinations of intra- and inter-group scramble and contest competitions" (Isbell and Young, 2002:181), second-generation models initially suggested that increased predator detection by group members, rather than food distribution, selected for sociality (van Schaik, 1983). Van Schaik's (1983) model, thus, argued that food abundance is only a secondary selective pressure, influencing social behavior within groups more than competition between them. Noting no positive relationship between food availability and group size (as would be predicted by Wrangham's model), van Schaik (1983) proposed the predation intra-group feeding competition (PFC) model, showing that when outcomes over food competition are tested using Wrangham's (1980) model, results indicate other factors are at work: namely, predation. Although fission-fusion species are typically excluded from these models (see below), Wrangham (1980) and van Schaik (1989) both emphasized the role female bondedness plays in the likelihood of agonistic interactions over high quality food supplies. In fact, van Schaik (1983:137) notes

> "Historically, fission-fusion groups are presumably derived from more coherent promiscuous (multi-male) groups that evolved towards a diet of high quality food found in small and scattered patches. The observation that they travel in bigger parties when food is abundant suggests that they too are trying to minimize predation risk, whenever circumstances will allow this."

Van Schaik (1989) later proposed particular ecological conditions that should produce four different types of primate groups, each with its own set of specific

aggressive tendencies. These predictions improved upon Wrangham's earlier one, though likewise neglected potential social factors influencing grouping behavior." Later studies on arboreal monkeys (Treves, 1999) and chimpanzees (Schultz et al., 2003) have further supported these models.

More recent models have returned to the idea of resource distribution as the determining factor of grouping. Isbell (1991) argued that clumped food distribution has widespread effects on ranging patterns that, in turn, influence how primates organize socially. In sum, then, all of these models emphasize the importance of ecological factors on a very primary level as the most important selection pressure on the evolution of female social relationships: Wrangham's early model stressed the importance of how foods are distributed, van Schaik focused on predation and only secondarily on food distribution and demographic and behavioral dynamics, and Isbell and colleagues suggested that food abundance (and distribution) as well as the costs of dispersal were the critical factors. Later influences on grouping behavior in primates have since been proposed. For example, considering the additional travel costs incurred with large groups (Chapman and Chapman, 2000), Janson and Goldsmith (1995) suggested that the amount of travel necessary can often predict group size. According to these authors, the spatial and temporal distribution of food availability affects movements, and therefore group size for most primates. This factor, although important in proximate influences on grouping behavior, is not thought to act on the evolution of social grouping. These initial ecologically-centered models, however, failed to account for additional social forces now thought to weigh significantly on the ultimate causes of gregariousness in primates. Sterk et al. (1997) have incorporated ecological aspects of the above models with added effects of habitat saturation and infanticide avoidance mechanisms by females to arrive at a new socioecological model. This newer model suggests that the external force uniting females is protection from infanticidal males, not predation risk (Sterk et al., 1997).

Finally, Isbell and Young (2002), in their "third generation" model, re-emphasized that, although the above-described models agree that ecological (e.g. food availability) variability influences female relationships, they do not necessarily agree on the exact nature of either the catalyst or consequence. They propose that quantitative measures of food

availability and competitive relationships, clearer definition of terms, and the teasing apart of co-variance between multiple factors will help us better understand independent effects of both habitat and sociality on female relationships (Isbell and Young, 1996, 2002). Despite the fact that chimpanzees show male philopatry and are typically excluded from the above models, understanding the dynamics of social organization is critical to teasing apart the influences on their own, unique, social system.

2.2 Potential Costs of Sociality

Despite the apparent benefits to sociality in primates, it is the balance between these benefits with accompanying costs that often determine the dynamics of any particular group (Wrangham et al., 1993). One of those potential costs is the increase in feeding competition (see above) that individuals will face when foraging in large groups on patchily distributed food sources (Wrangham, 1980). Another cost is infanticide, already observed in numerous primate species (baboons: Gomendio & Colmenares, 1989; chimpanzees: Stanford 1994a, 1994b, 1995; lemurs: Jolly et al., 2000; langurs: Hrdy, 1974, 2000; Boggess, 1979; howling monkeys: Clarke, 1983; Clarke et al., 1994) where non-paternal males are thought to target vulnerable infants fathered by rivals. Females, then, are thought to receive both benefits and costs in tolerating non-related males: In exchange for increased protection from these males, females make themselves more susceptible to infanticide (Sterk et al., 1997; Shimooka, 2003).

Hypotheses addressing how cooperative predator avoidance and infanticide risk affect grouping patterns in primates have been tested in the field, however, and not all results conform to predictions. For example, in one study on langurs *(Presbytis entellus),* group size was modified in response to predator density, with the number of males per group increasing as did potential threats (Treves & Chapman, 1996). Within the same group, analyses on infant survival rates showed no decrease in smaller groups, as might be predicted by the resource-defense hypothesis (Wrangham, 1980; Treves & Chapman, 1996;). Similarly, in his study on chimpanzee hunters and their favorite prey, red colobus monkeys (*Colobus badius tephrosceles)*, Stanford (1995a) found no significant difference in predator avoidance when he compared large and small groups of monkeys responding to chimpanzee hunting pressure.

Whether these inconsistencies are merely anomalies within the Order or representations of additional factors influencing group size is not yet known.

2.3 Fission-Fusion Sociality

Whereas most primates travel as all-inclusive groups chimpanzees *(Pan troglodytes* spp.) and spider monkeys *(Ateles* spp.) exhibit a unique social system (Chapman et al., 1993). Although both *Pan* and *Ateles* conform to the primate pattern in having one philopatric sex (in this case, males), their system of social organization, termed fission-fusion (Goodall, 1968), reflects one seemingly evolved to minimize intra-group feeding competition for specific dietary components (Klein & Klein, 1977; Wrangham et al., 1977; Wrangham 1980, 1986; Goodall, 1986; Symington, 1987; Chapman et al., 1994, 1995; Newton-Fisher et al., 2000; Anderson et al., 2002; Shimooka, 2003; but see Fedigan & Baxter, 1984[1]): namely, ripe fruit. In both species male cooperation and weak female bonds are seen (chimpanzees: Goodall, 1986; Mitani et al., 2001, but see Wittig & Boesch, 2003; spider monkeys: Symington, 1987, 1988) as well as distinct size differences in "core" areas, where individuals spend much of their time. Likewise both species show variability in community size [chimpanzees: from <25 (Sugiyama, 1981, 1984; Tutin et al., 1983) to more than 140 individuals (Boesch & Boesch-Achermann, 2000; Watts, 2003); spider monkeys: from <12 (Eisenberg, 1983) to >35 (Fedigan et al., 1988; see also Symington, 1987; Robbins et al., 1991; Wrangham et al., 1993; Chapman et al., 1995;], encompassing individuals all of which share a common territory and exhibit social tolerance (Goodall, 1986; Chapman et al., 1995). In both species females emigrate from their natal areas into neighboring ones at the onset of sexual maturity with males remaining in their natal communities, forming the core of communities.

Unlike most other primate groups, rarely will all individuals from a community of chimpanzees or spider monkeys aggregate in a single location (but see Suigyama, 1981, Table 4). Instead, individuals in both *Pan* and *Ateles* form smaller and more closely bonded assemblies, called either parties or subgroups that remain together for an indefinite time.

---

[1] Fedigan & Baxter (1984) found frequently that most male spider monkeys traveled in male-only parties.

Additionally, although some have proposed that strategic associative tendencies exist, especially for male chimpanzees (Newton-Fisher, 1999; Mitani et al., 2002), predictions of fluidity and alliances remain only partly understood by researchers.

The causes and consequences of living in fluid subgroups are almost as unpredictable as the groups themselves. As mentioned above, the major variables thought to predict grouping patterns best are predation pressure and resource competition, with ideal-sized groups those being ones that optimized an individual's inclusive fitness (i.e. cost of intragroup feeding competition exactly balanced with decreased risk of predation) (Rubenstein, 1980). Both of these variables have been investigated extensively in *Ateles* (Symington, 1987) and *Pan* (see more, Chapter Four), with studies on various communities examining how each of these socially-flexible species responds to variable ecological environments (Chapman et al., 1995). A brief review of these variables acting on *Ateles* party size is presented below:

Resource abundance

Ateles spend much of their time feeding on high quality, ripe fruits distributed in variable sized patches (Symington, 1987, 1988; Chapman, 1990a; Robbins et al., 1991; Chapman et al., 1994, 1995) and fruit abundance and party size have often been positively correlated (Klein & Klein, 1977; Symington, 1988; Chapman & Lefebvre, 1990; Chapman et al., 1995). Chapman & Lefebvre (1990) even found evidence that spider monkeys manipulate their group sizes with vocalizations to efficiently exploit specific fruit-rich sources. Studying spider monkeys in Columbia, Klein and Klein (1977) were one of the first to report on spider monkey social behavior in response to food abundance. They observed 80% of parties to consist of less than four individuals when food sources were dispersed compared to greater than eight individuals when they were patchy. Likewise, in Peru, Symington (1987) habituated and studied a single group of *Ateles paniscus chamek* at Manu National Park, discovering that there was a highly significant positive correlation between party size and fruit abundance. She further observed larger parties to travel further, thought to be a response to increased patch depletion time (Chapman and Chapman, 2000). Symington concluded that foraging party size in *Ateles* was easily adjustable to the energetic costs of being in larger

groups[2], however it has not yet been shown if and to what extent feeding group size is dependent on patch size [as has been shown in chimpanzees (Ghiglieri, 1984) and howling monkeys (Leighton and Leighton, 1982)]. Shimooka (2003), in her study on *Ateles belzebuth belzebuth* in Columbia, examined specifically the relationship between party size dynamics and fruit abundance in a single group. She found overall party size to be larger in fruit-abundant seasons, despite sex differences within the group [males exhibited relatively stable parties across seasons whereas females' party size was observed to fluctuate with seasonal fruit densities (Shimooka, 2003)].

Ranging

Few data are available on ranging in spider monkeys. In a study of two groups in Peru, one consisting of 40 individuals and the other of 37, average home ranges were significantly larger for males than for females (Symington, 1987). Females were thought to spend more time in "core areas" which were calculated to be about half the size of male's core range. Similar sex-different patterns have been seen in chimpanzees (Wrangham and Smuts, 1980). Symington (1987) suggested that the intragroup pressure associated with exploiting discrete patches of ripe fruit forced female spider monkeys (and chimpanzees) to forage solitarily, whereas territory defense and female monitoring caused males to include more area in their core range. It has also been hypothesized that dependent offspring prevent females from traveling as far as males (Wrangham and Peterson, 1996).

Differences between *Ateles* and *Pan*

Comparative studies, however, reveal subtle differences in how *Ateles* and *Pan* respond to ecological constraints (Chapman et al., 1995). Analyzing long term data from two habituated groups of spider monkeys and chimpanzees, Chapman et al., (1995) found that the two species differed in responses to two significant ecological categories: food resource density and distribution. Moreover, contrasts in reproductive strategies between the two species further complicated the comparison. Chimpanzee females exhibit conspicuous

[2] *Ateles*' traveling behavior is further complicated by their energetically expensive means of locomotion, i.e. brachiation

anogenital swellings, mate with multiple males, vocalize during copulations, and modify ranging patterns during their cycle (Wrangham & Smuts, 1980; Goodall, 1986; Wrangham et al., 1992; Chapman et al., 1995;), while spider monkey females are thought to conceal estrus and mate furtively (Klein, 1971; Symington, 1988; Chapman et al., 1995). As a result of this difference in female receptivity, male spider monkeys have evolved considerably different strategies than chimpanzees. Symington (1988), for example, suggests that male *Ateles* must either follow and defend individual females (much as chimpanzee males do – also called consortships [Manson, 1997]) or monopolize and defend resources likely to attract females.

The fluidity and flexibility of the fission-fusion social system, however, belies the potential costs it forces on some individuals. Larger parties travel farther (chimpanzees: Yamagiwa, 1999; Matsumoda-Oda, 2002; spider monkeys: Symington, 1987, 1988) and lower ranking animals are the first to defect from a group when a high quality food patch is insufficient to feed the entire group (Fedigan & Baxter, 1984). This is predicted when we consider that feeding rate does not change as a result of food source or party size (Symington, 1988; Chapman & Chapman, 1996). In sum, then, spider monkey and chimpanzee subgroup size appear to respond most reliably to seasonal variation, i.e. ecological changes (Chapman, 1990b; Robbins et al., 1991) as well as social dynamics.

Conclusion

The variables that interact to affect group size in primates are numerous and often overlap. The weight of these variables, however, may vary as does the season and/or particular social environment. For example, in the langurs *(Presbytis entellus)* mentioned above, Treves and Chapman (1996) concluded that conspecific threat was the most reliable predictor of group size and composition, suggesting that this selective pressure may also be acting on other social mammalian species as well. Certain factors, though, are likely to be less influential in certain species. In chimpanzees, for example, which because of their larger body size have fewer potential predators, predation pressure may affect social grouping less than other factors such as fruit abundance and cycling females (but see van Schaik, 1989). Nonetheless, the parallels demonstrated above between *Ateles* and *Pan* reveal how fission-

fusion species cope with and reconcile variations in ecological changes, adapting to circumstances with a social fluidity not seen in other species within the Order.

Sources

Anderson DP, Nordheim EP, Boesch C, Moermond TC. 2002. Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 90-101.

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Bradbury J, Vehrencamp S. 1976. Social organization and foraging in emballonurid bats. II. A model for the determination of group size. *Behav Ecol Sociobiol* 1:383-404.

Chapman CA. 1990a. Ecological constraints on group size in three species of Neotropical primates. *Folia Primatol* 55:1-9.

Chapman CA. 1990b. Association patterns of spider monkeys: the influence of ecology and sex on social organization. *Behav Ecol Sociobiol* 26:409-414.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: The importance of travel costs. In: Boinski S, Garber PA, editors, *On the move: How and why animals travel in groups,* Chicago and London: University of Chicago Press. p 24-42.

Chapman, C.A. & Chapman, L.J. 1996. Mixed-species primate groups in the Kibale Forest: Ecological constraints on association. *International J. of Primatol,* 17(1):31-50.

Chapman C, Lefebvre L. 1990. Manipulating foraging group size: spider monkey food calls at fruiting trees. *Animal Behaviour* 39:891-896.

Chapman CA, Wrangham RW, Chapman CA. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiology* 36:59-70.

Chapman CA, White FJ, Wrangham RW. 1994. Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors, *Chimpanzee Cultures*, Cambridge: Harvard University Press. p 41-58.

Chapman CA, White FJ, Wrangham RW. 1993. Defining subgroup size in fission-fusion societies. *Folia Primatol* 61:31-34.

Clarke MR, Sucker EL, Glander KE. 1994. Group takeover by a natal male howling monkey *(Alouatta palliate)* and associated disappearance and injuries of immatures. *Primates* 35(4):435-442.

Clarke MR. 1983. Infant-killing and infant disappearance following male takeovers in a group of free ranging howler monkeys *(Alouatta palliate)* in Costa Rica. *Amer J of Primatol* 5(3):241-247.

Eisenberg JF. 1983. *Ateles geoffroyi* (Species account). In: Janzen DH, editor, Costa Rican natural history, Chicago: The University of Chicago Press. p 451-453.

Fedgian LM, Baxter MJ. Sex differences and social organization in free-ranging spider monkeys *(Ateles geoffroyi). Primates* 25(3):279-294.

Fedigan LM, Fedigan L, Chapman C, Glander KE. 1988. Spider monkey home ranges: a comparison of radio telemetry and direct observation. *Amer J of Primatol* 16:19-29.

Frame LH, Malcolm JR, Frame GW, van Lawick H. 1979. Social organization of African wild dogs *(Lycaon pictus)* on the Serengeti Plains, Tanzania 1967-1978.

Ghiglieri MP. 1984. The chimpanzees of the Kibale Forest. New York: Columbia University Press.

Gomendio M, Colemares F. 1989. Infant killing and infant adoption following the introduction of new males to an all-female colony of baboons. *Ethology* 80(1-4):223-244.

Goodall J. 1968. Behaviour of free-ranging chimpanzees of the Gombe Stream Area. *Animal Behaviour Monograph* 1:163-311.

Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: The Belknap Press of Harvard University.

Holekamp KE, Cooper SM, Katona CI. Patterns of association among female spotted hyenas *(Crocuta crocuta). J of Mammal* 78(1):55-64.

Hrdy SB. 2000. The optimal number of fathers - Evolution, demography, and history in the shaping of female mate preferences. *Ann NY Acad Science* 907:75-96.

Hrdy SB. 1974. Male-male competition and infanticide among langurs *(Presbytis entellus)* of Abu, Rajasthan. *Folia Primatol* 22(1):19-58.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior in primates. *Behav Ecol* 2:143-155.

Isbell LA, Young TP. 2002. Ecological models of female social relationships in primates: Similarities, disparities, and some directions for future clarity. *Behaviour* 139:177-202.

Isbell LA, Young TP. 1996. The evolution of bipedalism in hominids and reduced group size in chimpanzees: alternative responses to decreasing resource availability. *J of Hum Evol* 30:389-397.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326-336.

Jarman PJ.1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.

Jolly A, Caless S, Cavigelli S. 2000. Infant killing, wounding and predation in *Eulemur* and *Lemur. Int J of Primatol* 21(1):21-40.

Klein LL, Klein D. 1977. Observations on two types of neotropical primate interact associations. *American Journal of Phys Anthro* 38:649-654.

Kruuk H. 1989. *The Social Badger: ecology and behaviour of a group-living carnivore* (Meles meles). Oxford: Oxford University Press.

Lee TM. 2004. *Octodon degus:* A diurnal, social, and long-lived rodent. *ILAR Journal* 45(1): 14-24.

Lefebvre D, Menard N, Pierre JS. 2003. Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. *Behav Ecol Sociobio,* 53(6):402-410.

Leighton M, Leighton DR. 1982. The relationship of size of feeding aggregate to size of food patch: howler monkeys *(Alouatta palliate)* feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14(2):81-90.

MacDonald DM., Stewart PD, Stopka P, Yamaguchi N. 2000. Measuring the dynamics of mammlian societies: an ecologists guide to ethological methods. In: Boitani L, Fuller K, editors, *Research Techniques in Animal Ecology: Controversies and Consequences,* New York: Columbia University Press.

Manson JH. 1997. Primate consortships - A critical review. *Current Anthropol* 38(3):353-374.

Matsumoto-Oda A. 1999. Mahale Chimpanzees: Grouping patterns and cycling females. *Amer J of Primat* 47:197-207.

Matsumoto-Oda A, Hayashi Y. 1999. Nutritional aspects of fruit choice by chimpanzees. *Folia Primatol* 70(3):154-162.

Matsumoto-Oda A, Osaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *Int'l J of Primatol* 19(6):999-1011.

McDaniel PS. 1995. The social behavior and ecology of the black-handed spider monkey *(Ateles geoffroyi)*. Unpublished Ph.D. thesis, Saint Louis University, St.Louis, MI.

Mitani JC, Watts DP, Pepper JW. 2002. Demographic and social constraints on male chimpanzee behaviour. *Animal Behaviour* 64:727-737.

Newton-Fisher NE 1999. Association by male chimpanzees: A social tactic. *Behaviour* 136:705-730.

Ottensmeyer CA, Whitehead H. 2003. Behavioural evidence for social units in long-finned pilot whales. *Can. J of Zoology* 81(8):1327-1338.

Richards AF. 1985. *Primates in Nature.* New York: W.H. Freeman and Company.

Robbins D, Chapman C, Wrangham RW. 1991. Group size and stability: Why do gibbons and spider monkeys differ? *Primates* 32(3):301-305.

Rubenstein DI. 1980. On predation, competition, and the advantages of group living. *Perspectives in Ethology* 3:205-231.

Rubenstein DI, Wrangham RW, eds. 1986. *Ecological Aspects of Social Evolution: birds and mammals.* Princeton, New Jersey: Princeton University Press.

Sussman RW. 1977. Feeding behavior of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH, editor, *Primate Ecology*, London: Academic Press. p 1-36.

van Schaik CP. 1983. Why are diurnal primates living in groups? *Behaviour* 87 120-144.

van Schaik CP. 1989. The ecology of social relationships among female primates. In: Standen V, Foley RA, editors, *Comparative Socioecology,* Cambridge: Cambridge University Press. p 195-218.

Schaller GB. 1972. *The Serengeti Lion: A Study of Predator-Prey Relations.* Chicago: Chicago University Press.

Shultz S, McGraw WS, Noe R. 2003. Primate social systems and predation risk: Factors influencing prey selection by crowned eagles in Tai National Park, Cote d'Ivoire. *American J of Phys Anthropol Suppl* 36: 191.

Shimooka Y. 2003. Seasonal variation in association patterns of wild spider monkeys *(Ateles belzebuth belzebuth)* at La Macarena, Colombia. *Primates* 44(2):83-90.

Sponge G, Stone J, Creel S. 2002. Genetic structure of lions *(Panthera leo L.)* in the Selous Game Reserve: implications for the evolution of sociality. *J Evolution Biol* 15(6):945-953.

Sterk EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291-309.

Stanford CB. 1995. The influence of chimpanzee predation on group-size and antipredator behavior in red colobus monkeys. *Animal Behaviour* 49(3):577-587.

Stanford CB, Wallis J, Mpongo, M. 1994a. E. Hunting decisions in wild chimpanzees. *Behaviour* 131:1-18.

Stanford CB, Wallis J, Matama H. 1994b. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. *Amer J of Phys Anthropol* 94(2):213-228.

Steenbeek R, van Schaik CP. 2001. Competition and group size in Thomas's langurs (Presbytis thomasi): the folivore paradox revisited. *Behav Ecol Sociobiol* 49(2-3):100-110.

Sugiyama Y. 1984. Population dynamics of wild chimpanzees at Bossu, Guinea, between 1976-1983. *Primates* 25(4):391-400.

Sugiyama Y. 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1976-1980. *Primates* 22(4):435-444.

Sussman RW. 1977. Feeding behavior of *Lemur catta* and *Lemur fulvus*. In: Clutton-Brock TH, editor, *Primate Ecology,* London: Academic Press. p 1-36.

Symington MM. 1987. Ecological and social correlates of party size in the black spider monkey, *Ateles paniscus chamek.* Unpublished Ph.D. thesis, Princeton, New Jersey: Princeton University.

Symington MM. 1988. Demography, ranging patterns, and the activity budgets of black spider monkeys *(Ateles paniscus chamek)* in the Manu National Park, Peru. *Amer J of Primatol* 15:45-67.

Treves A. 1999. Has predation shaped the social systems of arboreal primates? *International J of Primatol* 20(1):35-67.

Treves A, Chapman CA. 1996. Conspecific threat, predation avoidance, and resource defense: Implications for grouping in langurs. *Behav Ecol Sociobiol* 39(1):43-53.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

Waser PM, Zahavi, A. 1973. The importance of certain assemblages od birds as "information centers" for food hiding. *Ibis* 115:517-534.

Wittig RM, Boesch C. 2003. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *International J of Primatol* 24(4):847-867.

Wrangham R. 1986. Ecology and social relationships in two species of chimpanzees. In: Wrangham R, Rubenstein D, editors, *Ecological aspects of social evolution: birds and mammals,* Princeton: Princeton University Press. p 352-378.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham RW. 1977. Feeding behavior in chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor, *Primate Ecology*. London: Academic Press. p. 504-538.

Wrangham RW, Clark AP, Isabirye-Basuta G. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 81-98.

Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: Population density and day-range assays of exploitation competition. *Behav Ecol Sociobiol* 32:199-209.

Wrangham RW, Peterson D. 1996. *Demonic Males: Apes and the origins of human violence*. Boston: Houghton Mifflin.

Wrangham RW, Smuts BB. 1980. Six differences in the behavioural ecology of chimpanzees in the Gombe Stream National Park, Tanzania. *J Reprod Fert* 28:13-31.

Wright PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook Phys Anthropol* 42:31-72.

Chapter Three: Savanna chimpanzees

3.1 History

Initial long term studies on chimpanzees began in what was then called a "savanna" habitat (Goodall, 1968; Suzuki, 1969; Kano, 1971; Itani, 1977, 1979; McGrew et al., 1981). Most research today, however, concentrates on forest dwelling chimpanzees (Wrangham et al., 1992; Boesch and Boesch-Achermann, 2000; Mitani et al., 2002; Newton-Fisher, 2003) from East (Reynolds and Reynolds, 1965; Nishida, 1968; Kano, 1971; Wrangham, 1986) and West (Sugiyama and Koman, 1979; Boesch and Boesch-Achermann, 2000) African populations. Early foci in these studies included ecological descriptions and indirect evidence of social behavior, although have since progressed to habituation efforts and for some, the study of inter and intra-community dynamics, with a recent emphasis on aggression and sex-specific behaviors (Goodall et al., 1979; Boesch and Boesch, 1989; Manson and Wrangham, 1991; Stanford et al., 1994; Nishida and Hosaka, 1996; Wrangham and Peterson, 1996; Mitani and Watts, 1999; Wrangham, 1999; Watts, 2004; Wilson et al., 2004). While no savanna community has yet been fully habituated, well studied forested communities are now numerous. Further reinforcing the bias towards these communities, Boesch and Boesch-Achermann (2000) have suggested that the cultural attributes seen in some chimpanzees (e.g. Tai) may, in fact, be endemic to forested communities, the result of adaptive behaviors to tropical forest habitats.

Despite early foci on long term studies of forested chimpanzees, an increasing number of projects have recently begun centered on East and West African savanna populations and how community dynamics have evolved to suit such extreme ecological conditions (Figure 3.1.) (Moore, 1985, 1986, 1992; Hunt and McGrew, 2002; Pruetz, 2002; Pruetz et al., 2002). Despite critical differences [e.g. density (Kano, 1972; Baldwin et al., 1982; Moore, 1992), party stability (Tutin et al., 1983), diet (McGrew, 1983; McGrew et al. 1988)] between savanna and forest chimpanzees and the impact those differences may have on contemporary anthropological evolutionary theory, there remains considerably less information on savanna communities. There are two important reasons, however, why foci should center on these animals. First, populations here can provide us insight into how these apes adapt to life in marginal areas hypothetically characterized by less abundant and more

Fig. 3.1. Researcher walking through plateau during the dry season at Fongoli.

widely distributed food and water sources. Such adaptative strategies thus allow researchers to draw comparisons between forested and savanna chimpanzee communities. For example, whereas chimpanzees living in moist, tropical forests are rarely threatened with water scarcity (although see Lanjouw, 2002), savanna chimpanzees may face this problem for many weeks each year. Furthermore, because some savanna populations are not well protected, understanding the ecological value and behavioral influence of such sources can dramatically impact strategies for maintaining human-chimpanzee co-existence (Pruetz, 2002). Moreover, despite efforts to reveal ultimate causes of behavioral variation between communities (McGrew, 1992), researchers remain uncertain as to the pertinent environmental and cultural factors at work: Studies conducted on communities living under various conditions help shed light on each of the above-mentioned issues.

Secondly, becoming familiar with current savanna chimpanzee socioecology may provide insight into hominin evolution (see Chapter Four). Investigation of savanna chimpanzee ecology has been used to re-assess the evolution of bipedalism (Wheeler, 1985; Hunt, 1994; Richmond et al., 2001), behavioral characteristics of the last common ancestor

(McGrew et al., 1981; McGrew et al., 1982; Potts, 1987; Tanner, 1987; Moore, 1992, 1996), and physiological mechanisms necessary for moving from a wetter, arboreal life to a dryer, more bipedal one (Wheeler, 1985, 1993; Stanley, 1992; Hunt, 1994). With fossil evidence indicating hominins evolved in "extremely arid and open landscapes" (Reed, 1996:318), studying savanna chimpanzees who survive in similar ecological conditions allows researchers to observe selection pressures that may have acted on recent primate ancestors and consequentially, provides insight into what types of ecological and behavioral constraints may have been present at that time (Sept, 2002). As Moore (1996:281) summarized,

> "These differences between savanna woodland and more forested habitats may promote morphological, social or behavioral differentiation between savanna and forest chimpanzees (or facultative shifts in behavior among chimpanzees according to habitat at mosaic sites such as Gombe or Mahale). When such potential differentiation bears on traits considered important in human evolution, understanding of the bases for the differences – or their absence - can shed light on our scenarios of hominid behavioral ecology."

Chimpanzees living in such marginal habitats have become critical subjects of study for many different reasons and offer us a unique example of how complex these apes are (Suzuki, 1969; Kano, 1971). Specific adaptations to scarce resources may include undefined communal territories (Moore, 1992), reduced inter and intracommunal aggression, increased travel (Wrangham et al., 1992), or smaller daily and larger nesting mean party sizes (current study). We can generally predict, though, significant socioecological differences between apes living in these conditions and those living in moist forests. The current study sought to examine merely one aspect of these potential arid environment adaptations: daily and nesting party size.

Definitions and implications of 'savanna'

Considering the distribution of savanna-like habitats across the belt of equatorial Africa and the ecological variation between each one, establishing criteria distinguishing each one is necessary if these sites are to be compared (Kortlandt, 1983). One method of doing so is to quantify plant species diversity/density (Ellenberg and Mueller-Dombois, 1967; McGrew et al., 1981; Duvall, 2001). Typically, though, vegetational cover and mean

rainfall [annually around 1000mm for these sites (Moore, 1992)] are thought to be more important to wildlife, chimpanzees particularly (Moore, 1992; Duvall, 2000; Hunt and McGrew, 2002; Pruetz, 2002). Likewise, Kortlandt (1983) suggested "areal richness" calculations to standardize definitions. Nonetheless, quantitative ecological measures have not yet been universally employeed and as a result, researchers have struggled to resolve the origins of behavioral differences among chimpanzee populations. This is particularly important if we seek to extrapolate these differences to process working on hominin evolution. Despite queries over which measures define and distinguish savanna habitats, it remains likely that water, temperature, and canopy cover affect savanna chimpanzees significantly more than forest-dwelling chimpanzees (McGrew et al., 1981).

Fig. 3.2. Warthogs lounge in the middle of Parc National de Niokolo Koba in SE Sénégal

3.2 Socioecology of savanna chimpanzees

Resource abundance

Some ecological relationships have already been observed in savanna chimpanzee populations. At Ugalla (Figure 3.3.) and Mahale, Tanzania, Moore (1986:9) found that, "chimpanzee foods are concentrated along watercourses and escarpments, where drainage conditions permit the growth of evergreen *Ficus,* etc. and groves of larger trees and lianas."

These distribution patterns are expected to influence in which habitats chimpanzees spend much of their time and therefore feed. In a recent analysis of hair samples from Ugalla, Schoeninger et al. (1999) found indications that chimpanzees there are feeding primarily in wooded habitats rather than gallery patches or grassland. On a very superficial level, this contradicts McGrew et al.'s (1981) finding that chimpanzees bias their time in gallery forest patches to escape soaring temperatures in the extensive dry season in most savanna habitats.

Fig. 3.3. Overview of part of chimpanzee range in Ugalla, W. Tanzania (courtesy of Jim Moore)

It is thought that food and other surrounding resources limit and dictate much of animal behavior. With water sources drying and temperatures rising towards the middle and end of the dry season, chimpanzees must find different ways of adapting to such extreme periods. One way of doing this is by reducing energetically expensive activities. For example, in one community of chimpanzees, individuals were observed to spend more time on the ground during warm and dry months, and less time on the ground during wetter ones (Takemoto, 2004). It was concluded from this study that these chimpanzees were reducing thermoregulation costs by avoiding areas victimized by soaring temperatures (Takemoto, 2004). Increased time spent on the ground may make chimpanzees more susceptible to predation, but it has been suggested that increased visibility in savanna habitats may in fact nullify predation pressures (Moore, 1992).

Most socio-ecological models and fission-fusion social systems specifically address social behavioral adaptations to ecological conditions. Not all chimpanzee communities, however, have been shown to follow predicted behaviors. Studying a community of chimpanzees in Budongo Forest, Uganda, Newton-Fisher et al. (2000) demonstrated that party sizes there showed a negative or no relationship at all to food supply or distribution. This is not predicted for most forest communities and especially not for savanna communities where dispersed food supplies are thought to highly influence social and ranging behavior (Baldwin et al., 1982; McGrew, 1983; Tutin et al., 1983; McGrew et al., 1988; Moore, 1992; Duvall, 2000; see below). Such exceptions suggest a need to further investigate the behavioral adaptations to specific ecological conditions.

Ranging, Density, and Social Behavior

Ranging

The availability and distribution of resources determine not only where chimpanzees will spend the majority of their time but also where they will nest and the overall structure of their already flexible social system (Furuchi et al., 2001a, 2001b.; Mitani et al., 2001). For example, although home range size is predicted to increase with community size, habitat quality and demographic dynamics also play pivotal roles in ranging behavior (Wrangham, 1986; Moore, 1996; Herbinger et al., 2001). Moore (1985), in fact, suspected that savanna chimpanzees' range[1] is indeed water-presence dependent, dictating to where and what extent chimpanzees can travel. Examining the relationship between chimpanzee nest sites and permanent water sources, he found that most nests were located within ten kilometers of those sources, although some were identified as many as twenty kilometers away.

It has become clear with savanna chimpanzees that it is difficult to understand ranging patterns without a grasp of adjacent communities' boundaries. Typically more seasonal than forest habitats (Suzuki, 1969; Kano, 1971; McGrew et al., 1981; Moore, 1992;

[1] Defined as the area used by an individual chimpanzee over a specific time period (typically calculated annually, but see Newton-Fisher, 2003 [Baldwin et al., 1982; Goodall, 1986])

Hunt and McGrew, 2002), savanna habitats mandate that chimpanzees selectively exploit varying areas of their home range (Sugiyama and Koman, 1979; Baldwin et al., 1982). Ranging behavior and overall habitat use, for example (normally an artifact of food availability), may instead be the consequence of more widely distributed water and cover sources (McGrew et al., 1981). It should follow, then, that chimpanzee social organization responds accordingly. Conflicting results have been put forth regarding this topic, however. Tutin et al. (1983) observed no seasonal variation in party size across a four year study in SE Sénégal in the Parc National du Niokolo Koba. The authors propose, moreover, that, "A loose fission-fusion system would have difficulty operating in a home range of several hundred square kilometers. Once a party wanders off, simply locating other chimpanzees would be difficult; the community would be undefinable to an observer." In support of this, results from more recent studies suggest that, in fact, savanna chimpanzees may form larger parties and nest in larger groups (Hunt and McGrew, 2002). In doing so, chimpanzees would avoid having to relocate one another across great distances and ecological changes. This adaptation, however, would also have disadvantages, at least seasonally. When ripe fruit sources were more difficult to find, maintaining large party sizes would both increase scramble competition and consequently intra-community aggression (Wrangham, 1980; Isbell, 1991; Janson and Goldsmith, 1995). Likewise, parties would be forced to increase travel distance to find adequate food sources.

Deciphering just how savanna chimpanzees respond to such a mosaic of habitats remains a problem for those who study them. Although some have suggested that chimpanzees will be forced to range over larger areas just to include more widely distributed forest patches (Hunt and McGrew, 2002), others have gone so far as imagining a community of chimpanzees with a home range that may have borders indistinguishable to the chimpanzees themselves, with individuals instead establishing an undefined network of agonistically interacting parties that may show tactical association patterns (Newton-Fisher, 1999) but no discrete social boundaries (Moore, 1992). Despite early (Baldwin et al., 1982; Tutin et al., 1983; Moore, 1992) and recent (Hunt and McGrew, 2002) efforts to understand ranging patterns, no clear answers have yet emerged.

Despite the general consensus that savanna chimpanzees do have larger ranges than forest chimpanzees, researchers do not yet agree on what causes this behavior. Baldwin et al. (1982:382) proposed three factors that may provoke such an extensive range for the chimps they studied in Sénégal:

1. no geographical barriers prohibiting wide expansion,
2. the need to include more patchily distributed gallery forest in their range (see above), and
3. in times of water scarcity, the need to include and reach all possible water permanent or remaining water sources.

This last factor may work bidirectionally, though. That is, scarce water sources may limit a community's range by restricting how far any given individual can travel from a particular source. As mentioned above, Moore (1992) has already proposed one means of coping with such widely distributed food and water sources (e.g., boundary-less ranges). Other possibilities he suggested include communities whose parties (1) have lower frequencies of reunions, (2) that travel cohesively while maintaining vocal/visual contact, or (3) that use predictable routes.

Densities

As a result of expanded home ranges, savanna chimpanzees have been observed at densities considerably smaller than forest communities (Table 3.1; Kano, 1972; Baldwin, 1979; Baldwin et al., 1982; Moore, 1985; Goodall, 1986; Boesch and Boesch-Achermann, 2000; Pruetz et al., 2002), the latter as much as 50 times larger than the former (Baldwin et al., 1982; Pruetz et al., 2002). Even in tropical forests where different habitat types are seen, densities of individuals within the mosaic parts reflect the numbers seen at more open and arid sites.[2] Although one might expect the density of these animals to influence overall community size (see Table 3.1.), no trends have yet been observed (Tutin et al., 1983). Due to the difficulty in habituating and following savanna chimpanzees over this type of habitat, data on ranging remain elusive and ambiguous.

[2] Marchesi et al. (1995) found total density at Tai Forest, Ivory Coast to be 1.7 ind/km^2, but only 0.09 ind/km^2 within mosaic areas

TABLE 3.1. Reported densities for chimpanzees at 3 forested and 3 savanna sites

Community/Site	Indiv/km^2	Est. Comm. Size	Source
Forest			
Kasakela, Gombe	3-5	~60	Goodall, 1986
Budongo	2.12-2.22		Plumtre and Reynolds, 1996
Sonso, Budongo	3.2-6.8		Newton-Fisher, 2003
Tai	1.7	61	Boesch and Boesch-Achermann, 2000
Lac Tele, N. Congo	0.7	NA	Poulsen and Clark, 2004
Savanna			
Kasakati, Tanzania	0.5	45	Izawa, 1970
Filabanga, Tanzania	0.2	30-60	Kano, 1971
Ugalla, Tanzania	0.07-0.08	~40	Itani,1979
Semliki, Uganda	~0.89^	45	Hunt and McGrew, 2002
Fongoli, Sénégal	0.09	>26	Pruetz et al., 2002
Assirik, Sénégal	0.01-0.13	>21	Baldwin, 1979; Pruetz et al., 2002

^ calculated from Hunt and McGrew (2002)'s home range estimate of 50.1 km^2 and community size of 45

Social Behavior

Data reported on the social behavior of savanna chimpanzees are scarce. To learn about social dynamics, most researchers have had to use indirect means of assessing community and party sizes (minimum estimates, nesting parties, use of sociograms) (Tutin et al., 1983). At Assirik, Tutin et al. (1983) identified 21 different individuals in only 367 contacts over the four year project, with the largest party seen at one time being 22. Although largest party size can be a reflection of total community size (from 60% at Budongo (Sugiyama, 1968) to 100% [Sugiyama and Koman, 1979]), we do not yet know how direct ecological influences affect large grouping. It is hypothesized, however, that savanna chimpanzees will congregate in such large parties less often because of how their food sources are distributed (but see Tutin et al., 1983).

Presuming there was only one community at the Assirik site, Baldwin et al. (1982) estimated total community home range using three different methods. First, by connecting the farthest points with the shortest line between one recognized individual observed during the study, their first method yielded an estimated home range of 37.4 km^2. Doing the same for the distances between a single individual (adult male) gave them an estimate of 27.6 km^2.

The second method used the continuous distribution of sightings of chimpanzees,

which can occur within and outside the polygon. Connecting these points provided Baldwin et al. (1982) an estimate of 51.4 km^2 for the Assirik community. Kano (1971), in assessing potential home ranges of the chimpanzees of Filabanga, estimated ranges between 150-200 km^2, although he was unsure how many communities might coexist within this area.

Finally, when applying the same 'continuous distribution' method to the observed nests, the authors calculated an estimated home range of 72.1 km^2. However, none of these estimates suggested by the authors accurately represented what they thought to be the actual home range of this community. Instead, they asserted that if the minimum size of the community is divided by the estimated density, the home range would be about 239 km^2: one of the largest estimates given for any community of savanna chimpanzees (Baldwin et al., 1982; but see Kano, 1972). Applying this method to Fongoli, it is estimated that the focal community has a home range >300 km^2 (Pruetz, unpublished data).

3.3 Recent Developments in Long-Term Savanna Chimpanzee Behavioral Research

SAPP, Filabanga/Ugalla and Semliki

Only very limited and indirect data assessing the ecological influence on party size in savanna chimpanzees are available. In 1976-1979 work was conducted in Sénégal in an effort to explore the behavior and ecology of savanna dwelling chimpanzees living at Mt. Assirik, in the Parc National du Niokolo Koba (PNNK). The Stirling African Primate Project (SAPP), lasting only four years before it was arrested, found chimpanzees to nest in larger groups there than at other sites in Africa, though average observed party size (4.6 – Baldwin, 1979) was consistent with results from other studies (see above). Contact with chimpanzee parties showed significant seasonal and habitat-type trends [i.e., most sightings were in woodland habitats during the wet season and early dry seasons and in gallery forest during the middle and late dry seasons (Baldwin et al., 1982)]. Of 367 total chimpanzee contacts 267 yielded reliable party counts.

In Western Tanzania work has been conducted intermittently since the late 1960s (Suzuki, 1969; Kano, 1971, 1972; Nishida, 1989; Moore, 1994). Various sites have been explored (e.g. Filbanga, Kasakati, Ugalla), although at none have long term habituation

efforts been made (Moore, pers. comm.). Instead, short (9 days - Nishida, 1989) and long-term (23 months – Kano, 1972) surveys have been the norm, with researchers reporting on vegetation (Moore, 1994) mostly and indirect evidence of chimpanzee presence. Some have attempted to establish baseline data on chimpanzee social behavior. For example, at Kasakati, a team from Kyoto University encountered chimpanzee parties 206 times in 499 days, 119 of which lasted less than 30 minutes (no reported attempt was made to distinguish reliable from unreliable counts) (Suzuki, 1969). Expanding their searches in the area, Kano (1971, 1972) later reported chimpanzee presence throughout Western Tanzania, a region characterized by nutrient-poor soil and a deciduous woodland, termed "miombo" (Moore, 1992), with patchily distributed bush thickets, pockets of ever green forest, open grasslands, and swamps (Sept, 1998). In fact, Kortlandt (1983:235), in a rebuttle to McGrew et al.'s (1981) claim that Mt. Assirik was the driest chimpanzee habitat, concluded that,

> "From all this information it became obvious that it was not the Niokola-Koba but either the Faleme-Bafing area in Mali or the Ugalla area in Tanzania, which harboured the ecologically driest and most marginal chimpanzee habitat known."

Researchers working in these areas noted that chimpanzees exploit the heterogeneity of these different habitat types, seen best, for example, in the use of woodlands for fruits and seeds during the wet season, and the gallery forest pockets during the dry season to seek cover from soaring temperatures. How chimpanzees adapt their social structure to this type of habitat remains uncertain, although it has been suggested that common sleeping sites may allow individuals to remain in contact when nutritional needs demand greater daily ranges to find sufficient foods (See Discussion, Chapter Five).

More recently, long term projects focusing on savanna chimpanzees have been initiated and established in East Africa, namely at Semliki Wildlife Reserve in Western Uganda (Hunt et al., 1999; Hunt and McGrew, 2002) and in southeastern Sénégal (see below). Likewise, in 2001, researchers returned to Tongwe East Forest Reserve in Ugalla, Tanzania, where work has begun on diet, nest distribution, and ranging (Hernandez, pers. comm.). Results from Semliki indicate a possible community size there of 40-50 individuals and, again, minimal seasonal impact on party sizes (Hunt and McGrew, 2002). No estimates

are yet available for the Ugalla community (Hernandez and Moore, pers. comm.) and the results from Fongoli are reported in Chapter Five (see also Pruetz, unpublished data).

Southeastern Sénégal

The habitat in southeastern Sénégal has been described using the Ellenberg and Muller-Dombois (1967) characterization of plant formations (McGrew et al., 1981; Pruetz et al., 2002). The five initial habitat types[3] that early studies (Baldwin, 1979; McGrew et al., 1981; Baldwin et al., 1982; Tutin et al., 1983) used to categorize the ecology of the region are listed and described in Chapter Four. Of all the savanna chimpanzee study sites, southeastern Sénégal ranks as one of driest (although see Kortlandt, 1983; Sept, 1992) and most open with grassland and laterite plateau dominating the landscape, thus reducing both water availability and cover for chimpanzees (McGrew et al., 1981; Baldwin et al., 1982; Hunt and McGrew, 2002; Pruetz et al., 2002). Furthermore, although rainfall for 2003 was recently reported as > 1700 mm (Eaux et Foret, Departement de Kédougou, région de Tomboronokoto, pers. comm.), average annual precipitation is considerably lower. Moreover, the total accumulation of rainfall may be less critical to the surrounding wildlife than the distribution of it (McGrew et al., 1981).

Fongoli Chimpanzees

Seeking to expand on the findings of the SAPP work, Pruetz (2002) initiated a study on the Fongoli community of chimpanzees in 2001 in southeastern Sénégal, located 40 km from the PNNK (Figure 3.4.). Efforts are underway to habituate this community and behavioral data are recorded whenever possible (Pruetz, 2002). Early research in this region began in February 2000 when Pruetz et al. (2000) used nest counts to survey chimpanzees within and outside the PNNK. A total of 994 nests were identified outside the Parc versus 736 within it. Significant differences in nesting site as well as nest-nest proximity were found (Pruetz et al., 2002) with the authors concluding that the chimpanzees outside the PNNK frequently use non-forested areas for nest sites. This contradicted earlier findings (Baldwin,

[3] Pruetz et al. (2002) recently added a sixth type, described more in Chapter Four

Fig. 3.4. Fongoli village, in southeastern Sénégal

1979) suggesting gallery forest patches were highly preferred sleeping areas. Since then attention at Fongoli has centered, in part, on human-chimpanzee competition for the fruit *Saba senegalensis*, a major source of chimpanzee diet and human exploitation in the late dry season (Feb-June) (Pruetz, 2002; Knutsen, 2003; Pruetz and Knutsen, 2003). Knutsen (2003) examined *Saba* removal rates from the study area while exploring more sustainable agricultural practices for local people. Despite recent legislation providing protection for the chimpanzees within the area, the conflict between chimpanzees and humans remains a threat to each, with highly valued scarce resources being depleted at unsustainable rates.

Direct sustained observations of chimpanzees are rare in unhabituated communities, particularly those found in savanna habitats. Human observers are generally more easily detected from afar. Habituation efforts at Fongoli, however, have yielded strong progress in recording ranging patterns and individual identification within the Fongoli community. As of December 2003, 15 individuals had been identified and researchers had made a minimum community estimate of 26 chimpanzees based on known individuals (Pruetz, unpub. data). Contacts with chimpanzees have lasted as long as nine hours and repeated contact with parties is now typical, indicating that chimpanzees are responding positively to habituation efforts (Pruetz, unpublished data). Prior to the current study, mean party size at Fongoli was

found to be 3.1, significantly lower than reports from other sites (see Chapter Five, Table 5.2; Boesch and Boesch, 2000, Table 5.2).

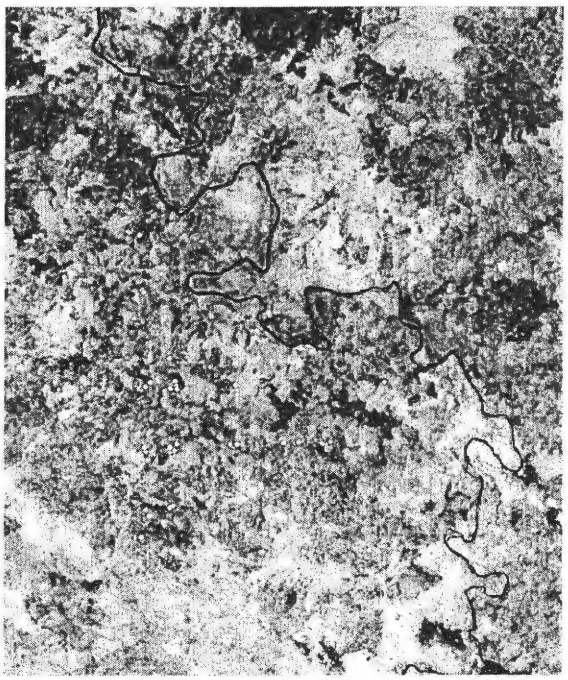


Fig. 3.5. Satelite image taken of the Fongoli study area. Black line indicates the Gambia River; yellow circles represent individual nest groups from 2002; Red regions are open areas (agricultural fields, natural plateaus) with green reflecting covered ones (woodland) (from Clapp, 2004).

Conclusion

In sum, research centering on savanna chimpanzee behavioral ecology has begun to grow. Current projects in East and West Africa are indicative that future comparisons will soon be made between savanna populations living in various degrees of marginal habitats (see above) as well as to forested communities. Although data on social behavior lag due to habituation levels, indirect data on ranging, feeding ecology, and nesting behavior are currently being recorded at the four sites, in four different countries (see Figure 1.2., Chapter 1). Despite these forthcoming data, there remain critical questions regarding savanna chimpanzee socioecology. Most importantly for the current study are those pertaining to social behavioral adaptations (e.g. day and nest party size) to widely distributed food sources. As questions addressing ecological variation and consequent behavioral modification pervade this work so do research efforts to better understand both proximate and ultimate

adaptive mechanisms for these apes. It is with the goal of contributing to those efforts and our overall understanding of savanna chimpanzees that the current study was conducted.

Sources

Baldwin PJ. 1979. The natural history of the chimpanzee *(Pan troglodytes verus)* at Mt. Assirik, Sénégal. Unpublished Ph.D. thesis, Stirling: University of Stirling.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *International J of Primatol* 3(4):367-385

Boesch CA, Boesch-Achermann H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Amer J of Phys Anthropol* 78:547-573.

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Clapp AG. 2004. Human and non-Human Primate Conflict: An investigation of causes, effects, and solutions. Unpublished Masters Thesis, Austin: University of Texas, Austin.

Duvall CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21(4):173-203.

Duvall CS. 2001. Habitat, conservation, and use of *Gilletiodendron glandulosum* (Fabacae, Caesalpinoideae) in southwestern Mali. *Syst Geogr* 71:699-737.

Ellenberg H, Mueller-Dombois D. 1967. Tentative physiognomic-ecological classification of plant formation of the earth. *Berichte de Geobotanischen Institutes der Eidgenossischen Technische Hochschule Stiftung Rubel* 37:21-46.

Furuichi T, Hashimoto C, Tashiro Y. 2001a. Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees *Int J of Primatol* 22(6):913-928.

Furuichi T, Hashimoto C, Tashiro Y. 2001b. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. *Int J of Primatol* 22(6):929-945.

Goodall J. 1968. Behaviour of free-ranging chimpanzees of the Gombe Stream Area. *Animal Behaviour Monograph* 1:163-311.

Herbinger I, Boesch C, Rothe H. 2001. Territory Characteristics among three neighboring chimpanzee communities in the Tai National Park, Cote d'Ivoire. *Int'l J of Primatol* 22(2):143-167.

Hunt K. 1994. The evolution of human bipedality: ecology and functional morphology. *J of Human Evolution* 26:183-202.

Hunt KD, Cleminson AL, Latham J, Weiss RI, Grimmond S. 1999. A partly habituated community of dry habitat chimpanzees in the Semliki Valley Wildlife Reserve, Uganda. *Amer J of Phys Anthropo* Supply. 28,157.

Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Mont Assirik, Sénégal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 35-51.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior in primates. *Behav. Ecol* 2:143-155.

Itani J. 1977. Evolution of primate social structure. *J of Human Evolution* 6:235-243.

Itani J. 1979. Distribution and adaptation of chimpanzees in an arid area. In: Hamburg DA, McCown ER, editors, *The Great Apes,* Menlo Park: Benjamin/Cummings. p 55-74.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326-336.

Kano T. 1971.The chimpanzees of Filabanga, Western Tanzania. *Primates* 12:229-246.

Kano T. 1972. Distribution and Adaptation of the chimpanzee on the Eastern shore of Lake Tanganyika. *Kyoto University African Studies* 7:37-60.

Knutsen, PG. 2003. Threatened existence: *Saba senegalensis* in southeastern Senegal. Unpublished MA thesis, Ames: Iowa State University.

Kortlandt A. 1983. Marginal habitats of chimpanzees. *J Human Evolution* 12:231-278.

Lanjouw A. 2002. Behavioural adaptations to water scarcity in Tongo chimpanzees In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 52-60.

Manson J, Wrangham R. 1991. Intergroup aggression in chimpanzees and humans. *Curr Anthropol* 32:369-390.

Marchesi P, Marchesi N, Fruth B, Boesch C. 1995. Census and distribution of chimpanzees in Cote D'Ivoire. *Primates* 36(4):591-607.

McGrew WC. 1983. Animal foods in the diets of wild chimpanzees: Why cross-cultural variation? *J of Ethology* 1:46-61.

McGrew WC. 1992. *Chimpanzee Material Culture*: Cambridge University Press: Cambridge.

McGrew WC, Baldwin PJ, Tutin CEG. 1988. Diet of wild chimpanzees *Pan troglodytes verus)* at Mt. Assirik, Sénégal: I. Composition. *Am, J. of Primatol* 16:213-226.

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirk, Sénégal, West Africa. *J of Human Evolution* 10:227-244.

McGrew, W.C., Sharman, M.J., Baldwin, P.J., & Tutin, C.E.G. 1982. On early hominid plant-food niches. *Current Anthropology* 23: 213-214.

Mitani JC, Watts DP. 1999 Demographic influences on the hunting behavior of chimpanzees. *American J of Phys Anthropol* 109(4):439-454.

Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol* 11(1):9-25.

Moore, J. 1985. Chimpanzee Survey in Mali, West Africa. *Primate Conservation* 6: 59-63.

Moore, J. 1986. Arid Country Chimpanzees. *AnthroQuest*. 36: 8-10.

Moore J. 1992. 'Savanna chimpanzees'. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 99-118.

Moore J. 1994. Plants of the Tongwe East Forest Reserve (Ugalla), Tanzania. *Tropics* 3(3/4):333-340.

Moore J. 1996. Savanna chimpanzees, referential models and the last common ancestor. In: McGrew WC, Marchant L, Nishida T,editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 275-292.

Newton-Fisher NE. 2003. The home range of the Sonso community of chimpanzees from the Budongo Forest, Uganda. *Afr Journal of Ecol* 41(2):150-156.

Newton-Fisher NE, Reynolds V, Plumptre AJ. 2000. Food supply and chimpanzee *(Pan troglodytes schweinfurthii)* party size in the Budongo Forest Reserve, Uganda. *International J of Primatol* 21(4):613-628.

Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.

Nishida T. 1989. A note on the chimpanzee ecology of the Ugalla Area, Tanzania. *Primates* 30(1):129-138.

Nishida T, Hosaka K. 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 114-134.

Plumtre D, Reynolds V. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. *Int J Primatol* 17:85-99.

Potts R. 1987. Transportation of resources: Reconstructions of early hominid socioecology: a critique of primate models. In: Kinsey W, editor, *The evolution of human behavior: Primate models,* Albany: State University of New York Press. p 28-50.

Poulsen JR, Clark CJ. 2004. Densities, distributions, and seasonal movements of gorillas and chimpanzees in swamp forest in northern Congo. *Int'l J of Primatol* 25(2):285-306.

Pruetz JD. 2002. Competition between savanna chimpanzees and humans in southeastern Sénégal. *Amer J Phys Anthropol* 128-128 Suppl. 34 2002

Pruetz JD, Knutsen P. 2003. Scrambling for a common resource: Chimpanzees, humans, and *Saba senegalensis*, in southeastern Sénégal. *Amer J Phys Anthropol* 172-172 Suppl. 36

Pruetz JD, Marchant LF, Arnot J, McGrew WC. 2002. Survey of chimpanzees *(Pan troglodytes verus)* in southeastern Sénégal. *American J of Primatol* 58:35-43.

Reynolds V, Reynolds F. 1965. Chimpanzees in the Budongo Forest. In: Devore I, editor, *Primate Behaviour,* New York: Holt, Rinehard and Winston. p 368-424.

Richmond BG, Begun DR, Strait DS. 2001. Origin of human bipedalism: The knuckle-walking hypothesis revisited. *Yearbook of Phys Anthropol* 44:70-105.

Schoeninger MJ, Moore J, Sept JM. 1999. Subsistence strategies of two "savanna" chimpanzee populations: The stable isotope evidence. *American J of Primatol* 49(4):297-314.

Sept J. 1998. Shadows on a changing landscape: Comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American J of Primatol* 46(1):85-101.

Sept J. 2002. Chimpanzees on the edge: The implications of chimpanzee ecology in "savanna" landscapes for hominid evolution. In: Contreras JM, Véa JJ, editors, *Primates: Evolucion, Cultura Y Diversidad,* p 51-68.

Stanford CB, Wallis J, Matama H. 1994. Patterns of predation by chimpanzees on red colobus monkeys in Gombe National Park, 1982-1991. *Amer J of Phys Anthropol* 94(2):213-228.

Stanley SM. 1992. An ecological theory for the origin of *Homo. Paleobiology* 18:237-257.

Sugiyama Y. 1968. Social organization of chimpanzees in the Budongo Forest, Uganda. *Primates* 9:225-258.

Sugiyama Y, Koman, J. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20(3):323-339.

Suzuki A. 1969. An ecological study of chimpanzees in a savanna woodland. *Primates* 10:103-148.

Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *Am J of Phys Anthropol* 124(1):81-92.

Tanner NM. 1987. Gathering by females: the chimpanzee model revisited and the gathering hypothesis. In: Kinsey E, editor, *The Evolution of Human Behavior: Primate models,* Albany: State University of New York. P 3-28.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

Watts DP. 2004. Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int'l J of Primatol* 25(3):507-521.

Wheeler PE. 1985. The loss of functional body hair in man: the influence of thermal environment, body form and bipedality. *J of Human Evolution* 14:23-28.

Wheeler PE. 1993. The influence of stature and body form on hominid energy and water budgets; a comparison of *Australopithecus* and early *Homo* physiques. *J of Human Evolution* 24:13-28.

Wilson ML, Wallauer WR, Pusey AE. 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *Int'l J of Primatol* 25(3):523-549.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham RW. 1986. Ecology and social relationships in two species of chimpanzees. In: Wrangham RW, Rubenstein D, editors, *Ecological aspects of social evolution: birds and mammals,* Princeton, New Jersey: Princeton University Press. p 352-378.

Wrangham RW. 1999. Evolution of coalitionary killing. *Yearbook of Phys Anthropol* 42:1-30.

Wrangham RW, Clark AP, Isabirye-Basuta G. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics in Primatology Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 81-98.

Chapter Four: Distribution of foods

(For an introduction on ecological influences on grouping behavior in primates, chimpanzees specifically, see Chapter Two)

Introduction

4.1 Importance of ecological typing for hominin evolution and the role of savanna chimpanzees

The ecological features of savanna habitats have long been examined in relation to the evolution of modern humans. Dart (1925) was one of the first to invoke environmental change as the turning point for the arrival of the genus *Australopithecus* and later *Homo,* broadly concluding in later work that more open and xeric regions were the ultimate causes of hominin species origination and extinction. Recent analyses of paleoecology have supported his claims, suggesting distinct correlations between mammalian densities and climatic change over the last few million years, especially in tropic-located communities (Reed, 1997). These relationships indicate that climatic, and consequently ecological, change may have been the catalyst for the emergence of the genus *Homo*. The gradual modification of southern and East African mesic forests, to drier, more open wooded grasslands that would eventually select for the evolution of bipedalism in early species of Hominidae. Stanley (1992:250) summarizes: "It is reasonable to conclude that only a profound environmental change might have disrupted the *Australopithecines'* highly successful adaptive complex."

Australopithecus and *Homo* evolution, then, have been greatly influenced by environmental change. Likewise, earlier primate lineages probably faced ecological changes that caused speciation or, at the very least, particular behavioral adaptations. We know, for example, that modern chimpanzees are most bipedal in habitats closely resembling those that existed during the middle to late Miocene, when Australopithecines were common (Hunt, 1994). One

proposed hypothesis, then, is that this positional behavioral (and later anatomical development) evolved as a response to the location of valuable foods, and not other selection

pressures. Reed (1997), using fossil assemblages from numerous sites across eastern and southern Africa, demonstrated that around 1.8 milllion years ago (mya) there was a 30% increase in Bovidae species, a likely result of a reduction in moist forests and expanded open woodlands and grasslands. It is thought that this significant environmental shift affected frugivorous species more than others, selecting for less arboreal, more efficient terrestrial travelers who would have to cover greater distances in search of ripe fruits. Actual features of these past ecosystems are generally unknown, but it is thought that they may have resembled current "savanna" areas, such as those in southeastern Sénégal, western Uganda, or western Tanzania. As a result, studying savanna chimpanzees may provide clues into how highly social, large-bodied primates adapt to such areas.

One way of doing this is to examine feeding tree distribution. Although previous studies have often measured food abundance (see Chapter Five for review), the extreme conditions of savanna regions are thought to make food distribution equally, if not more important in affecting grouping patterns. The current study measured the distribution of critical food sources to the Fongoli community of chimpanzees as a means of exploring how these apes adapt to such a diverse and challenging habitat.

4.2 Methods

The current study focused on the Fongoli community of chimpanzees in southeastern Sénégal (12°55'N 16°02'W). This region has been characterized as a Sudanian-Guinean mosaic habitat, composed mainly of woodland-savanna, and broken up by large stretches of lunar plateau and pockets of gallery forest (McGrew et al., 1981; Hunt and McGrew, 2002). The village of Fongoli (Chapter Five, Figure 5.5.) lies 6 km NW of the regional capital of Kédougou and <50 km SE of the Parc National du Niokolo Koba (PNNK), not far from the Malian (~ 85 km) or Guindean (~35 km) borders. Permission to conduct research in the area has been granted to Jill Pruetz by the Department du Eaux et Forets du Sénégal, as well as by local tribal leaders of the surrounding villages.

History

Systematic efforts to explore savanna chimpanzee behavioral ecology began in the late 1970s with the Stirling African Primate Project (SAPP). Working inside the Parc National du Niokola Koba, researchers focused on diet, ranging, and social behavior in a wild community of non-habituated chimpanzees. Aborted after four years because of poor habituation progress, research was re-established in this region in 2000 when Pruetz et al. (2002) initiated a survey comparing chimpanzee densities within and outside the PNNK's boundaries. Known as the Miami African Primate Project (MAPP), it found that chimpanzee densities had risen within the Parc's boundaries since the SAPP work of the late 1970s and more importantly, results indicated that chimpanzee densities were possibly as high as 0.09 individuals/km^2 outside the Parc (compared to 0.13 individuals/km^2 within the PNNK) in areas where chimpanzees would have to compete with local villagers for scarce water and fruit resources (Pruetz, 2002; Pruetz et al., 2002; Knutsen, 2003). Further investigation found that chimpanzees in this region of Sénégal are rarely hunted and have learned to co-exist with people of the surrounding villages. As a result of these findings, a long term project was established in 2001 in and around the village of Fongoli within the Tomboronkoto region. The project's current objectives are to habituate a community of chimpanzees while also examining aspects of human-chimpanzee competition for limited resources (Pruetz, 2002;

Pruetz & Knutsen, 2002; Knutsen, 2003). Ultimately the project aims to examine the effect of savanna food resources on chimpanzee behavior and social organization.

These initial studies on chimpanzees in Sénégal classified habitats according to Ellenberg and Mueller-Dombois's (1967) "physiognomic classifications" of plant formations which sought to describe various ecological areas to allow for cross-site comparisons. In the last half-century, however, specific studies on West African ecology have exposed the diversity such 'savanna' areas provide. Adam (1965:159), in fact, suggested that Sénégal has "excessive variation," with the north exhibiting patterns that mimic Sahelian areas versus the south which showed more Guinean, with patches of forest much like those found in equatorial countries. Rainfall, he speculated, was what caused such differences, with ranges from 400 mm annually in the north to >1800 mm annually in the south. It was concluded that Sénégal has three distinct regions with four transition domains intertwining them (Adam, 1965).

More recent work has concentrated on classifying vegetation types in Sénégal, seeking to confirm or refute early suggestions by White (1983), who used floristic, photgeographical, and physiognomic parameters in his survey of much of Africa. Efforts have centered on establishing guidelines for what constitutes particular vegetation 'types' (e.g. woodland, grassland, etc.) and then assessing particular regions of the country (Frederiksen and Lawesson, 1992). Frederiksen and Lawesson (1992) initially classified seven different vegetation types and patterns in Sénégal (Appendix A), but later work by Lawesson (1995:51) classified more than eight in SE Sénégal alone, most dominated by a single species (i.e. "*Acacia dudgeoni* bushland"). Despite his efforts, entire areas were often labeled as "woodland bushland mosaics", demonstrating well the diversity of habitat structure in this region. The current study followed earlier work in the area (McGrew et al., 1981; Pruetz et al., 2002) in classifying habitats.

Study Site

The study area itself is a 50 km^2 region and contains three villages: the smallest (Fongoli) being home to <50 people and the largest (Djenji) <500 (pers. obs.). Between these

villages much of the land is heavily disturbed by people from the encompassing villages and also those from Kédougou (Figure 4.1.), who have established agricultural fields throughout the area (Knutsen, 2003). Because the study period was limited to seven months, if and how often chimpanzees use uninhabited crop fields and whether party size was adjusted because of that could not be assessed. It is thought, however, that all animals typically avoid these rather open areas for the same reasons they avoid plateaus (predation and heat). Human presence is seen throughout the area during all months. Most hunters await potential game at valued water sources and appear to prefer warthog *(Phacochorus aethiopicus)* and monkey *(Cercopithecus aethiops* and *Erythocebus patas)*, avoiding chimpanzee in response to cultural traditions (Clavette, 2003). Overall resource competition between humans and nonhumans is thought to be highest during late dry seasons when food and water availability are predictably low for all organisms (Duvall, 2000; Pruetz, 2002).

Fig. 4.1. Map of Sénégal, Kédougou is located in the southeast part of the country

Ecological Sampling

Known feeding tree distribution was examined throughout the core range of the Fongoli community. Each known feeding tree (N=75 at the time of the study) was located and the surrounding area divided into four 90 degree quadrants (Barbour et al., 1999). Within each quadrant the nearest tree of the same species as the feeding one was sought and the distance between the two measured. Where it was impossible or dangerous to safely travel[1] between trees the approximate distance was estimated to the nearest 0.5m (following Duvall, 2000). The average distance was then taken for all four data points and used to calculate total density of the particular species within a pre-determined area (in this case, the 50 km^2 core range study site). From these data the density of a particular tree species can be extrapolated and mapped onto an entire region. This procedure follows Cottam and Curtis (1956) and Barbour et al.'s (1999) description of point-center quarter (PCQ) ecological sampling. Advantages of this method include its efficiency in reducing error, especially versus rival methods such as the more simplified nearest neighbor method (Cottam & Curtis, 1956). Although PCQ can also be problematic if there exist sudden and significant changes in slope. Such slope changes did occur in two instances when measuring distances between trees, but neither are thought to be significant in affecting final calculations.

Objectives

Objectives included obtaining data from ten different feeding trees of each known species. However, considering the aversive nature of the chimpanzees, feeding trees were not easily identified. A tree was only considered a feeding source if researchers observed an individual chimpanzee eating an identified part of the tree. Indirect evidence such as food remains were also recorded although not used for analysis. When sample size of a particular species did not meet the above-criteria (i.e. if only seven known feeding trees existed for that species), the remaining three were identified by selecting the first of that species that fell within five meters of a pre-established transect. This method was chosen to control for bias and reach the desired sample size. In total, 94 trees were identified and measured, of which 23 were systematically sampled: six species of known feeding trees met criteria: *Saba*

[1] This happened only two times, both when uncrossable rivers prevented exact measurement

senegalensis, Pterocarpus erinaceus, Adansonia digitata, Hexalobus monopetalus, Baissea multiflora, and *Ficus* spp. (see *TABLE 4.2*).

4.2b Habitat – Flora

Present day African habitats are often broadly characterized, with most descriptions of habitat types yet to be universal endorsed. For example, 'forest' may indicate anything ranging from lowland tropical ones to those montane areas found at higher latitudes. The flora and overall vegetation distribution and composition of Southeastern *Sénégal* have not been studied extensively, although there exist various reports examining the physiognomic and ecological identification of plant arrangement (Ellenberg & Mueller-Dombois, 1967) and also overall phytogeographical patterns throughout the country (Lawesson, 1995). High species diversity within the country is attributed to the various habitats which range from multiple types of woodland to valleys characterized by patches of dense gallery forest, often connected by vast stretches of sandstone and laterite plateau. In many ways this habitat mimicks that of Western Tanzania where earlier studies of savanna chimpanzees were conducted (Kano, 1971; Nishida, 1989). This diverse array of habitat types found mostly in the southeastern portion of *Sénégal* has been identified and labeled as woodland bushland mosaic to account for the various forms of ecology present to surrounding wildlife (Frederiksen & Lawesson, 1992).

The current study used structural patterns (i.e. canopy cover, dominant tree height, and extent of undergrowth) (Marchesi et al., 1995) and followed that of Pruetz et al. (2002), using Ellenberg & Mueller-Dombois' (1967) classification of savanna areas. Baldwin et al. (1982) classified five types of habitat within this heterogeneous and alluvial Sudanian savanna-woodland of Sénégal during the SAPP: Bamboo, grassland, woodland, plateau and gallery forest, with the last of these comprising the most fertile habitat available to the chimpanzees (McGrew et al., 1981, 1988; Hunt & McGrew, 2002). A fifth type, ecotone, was later added to include evergreen wooded vegetation habitat created from water run-off (Pruetz et al., 2002). The descriptions that follow in this section adhere to those used by Baldwin et al. (1982), Lawesson (1995), and Hunt & McGrew (2002), although are modified slightly to account for the impact of season on habitat characterization (see "grassland"

specifically). It is yet unclear how much 'savanna' areas such as Fongoli resemble those on other parts of the continent, e.g. Ugalla. For example, in a brief survey of chimpanzees in Western Tanzania, Nishida (1989:132) classified only four different types of habitat: savanna, woodland, forest, and valley bottoms. Whether or not these "savannas" resemble the plateaus from Fongoli cannot be said for sure, but researchers seem reasonably confident that critical areas for chimpanzees, namely gallery forest patches, do play similar roles across communities.

Gallery Forest

Gallery forests typically harbor high densities of azonal plants and are thought to be the most important habitat type to local chimpanzee populations (Duvall, 2000; Hunt & McGrew, 2002), although they typically represent the smallest proportion of total habitat (3% at Assirik – Hunt & McGrew, 2002; and 1% at Filabanga – Kano, 1971). These Sudanian pseudo-forests were initially thought to be located only in sultry river valleys (Kano, 1971; Lawesson, 1995), characterized by *Crateva, Cola, Pterocarpus and Lonchocarpus* (and *Cynometra* in East Africa – Nishida, 1989), but their patchy presence in Sénégal indicates this may not always be the case (pers. obs.). Only in Western Tanzania where a different type of forest area (characterized by *Carapa)* is found at higher altitudes have they been considered "montane" (Nishida, 1989). At Fongoli these small pockets of shaded forests are characterized by high canopy (between 10-40m), as well as *Cola, Ficus* and *Diospyros* growing out of steep, water-course valleys in between large laterite bolders (Lawesson, 1995; Duvall, 2000; Hunt & McGrew, 2002). These areas are known for having interlocking tree crowns which offer refuge in the form of permanent water sources and shade. Moreover, Duvall (2001) has noted that the dominant genus of Baffing Reserve in southwestern Mali, *Gilletiodendron,* may offer microclimates for nearby chimpanzee communities.

It is undisputed that these habitats are critical for chimpanzees who live in such arid regions. For example, despite making up the smallest proportion of habitat, gallery forests hosted the most observations of chimpanzees during the SAPP work in the late 1970s (54%, Tutin et al., 1983, Table 7)[2].

[2] It is worth noting here that time spent in each habitat was NOT controlled for in this analysis

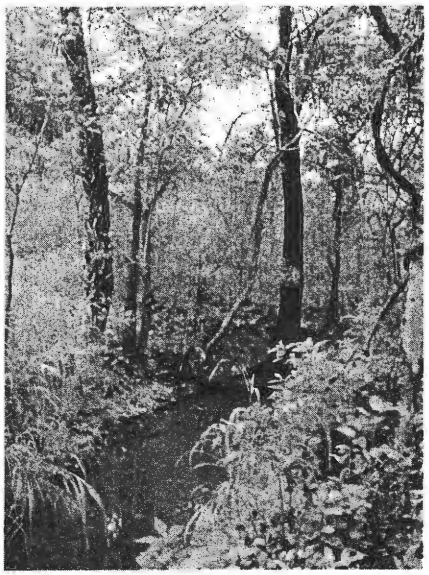
Ecotone and Marigot (Figures 4.2., 4.3.)

Neither ecotone nor marigot habitat types were used in earlier descriptions of these habitats (Baldwin, 1979; McGrew et al., 1981). Ecotone was introduced by Pruetz et al. (2002) to describe the area created from plateau water runoff that resulted in ribbons of evergreen woody vegetation along plateau edges. Often times these ecotone habitats transition into gallery and terminate at small streams or rivers characterized by lush, overgrown 'elephant grass' which remains damp for considerable time into the early and even mid dry season. (pers. obs.). This type of vegetation has been observed to "burn spectacularly" (Hunt and McGrew, 2002:38) when it is found in open grasslands. Marigots are technically a type of woodland, but here will be considered with ecotone because of their shared proximity to water sources. Marigot areas typically line streams that are used year round by chimpanzees and possibly other primates as well. During the wetter months much of the wildlife is thought to exploit these abundant sources which wind their way throughout the study area. When these streams dry up, though, chimpanzees have been seen to dig wells on their soft, sand-layden surface in search of water (Figure 4.5.; Hunt and McGrew, 2002). Although this behavior has not yet been seen by researchers at Fongoli, indirect evidence remains prevalent during the drier months when alternative water sources may be difficult to locate (Stewart, pers. obs.)

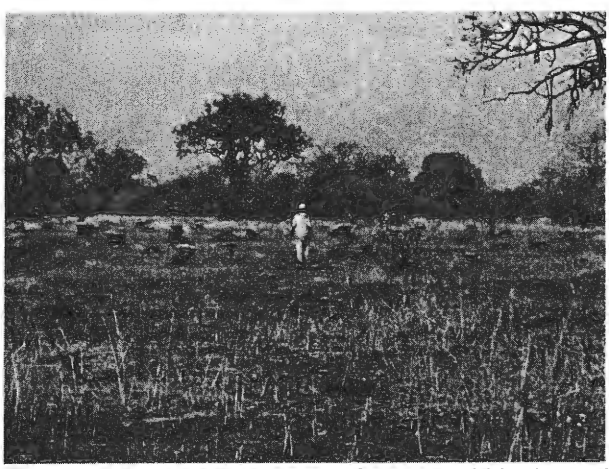
Plateau (Figures 4.4., 4.5.)

Hunt & McGrew (2002:38) described these vast stretches of plateau as being "lunar" where "little vegetation can thrive." With wide and long corridors of flat, obdurate terrain scattered with laterite rocks and little vegetation taller than 1 meter. With the onset of rains there grows *Rhtachne triaristata* blanketing these stretches to the perimeter and even pervading into the adjacent woodlands that contain them. Rarely are chimpanzees seen crossing these plateaus, preferring instead to travel through the more dense and protected woodlands and wooded grasslands (see below) that line the perimeter. Often times pockets form between the laterite rock that contain small pools of water. These may provide water sources for chimpanzees, however their assured exposure to daily sunlight during the dry

season results in relatively quick evaporation (pers. obs.).



Figures 4.2. and 4.3. Example of marigot habitat during the wet season. Chimpanzees may use these areas as abundant water sources until the streams run dry when the apes begin digging through top soil layers (right), essentially creating wells.



Figures 4.4. and 4.5. Example of plateau within the study site during dry (left) and wet seasons

Grassland

Like gallery forest, grasslands represent the small proportion of the habitat within the Fongoli's community range (pers. obs). Baldwin et al. (1981) described these areas at Mt. Assirik as narrow-leaved savannas with widely distributed deciduous trees, while Hunt &

McGrew (2002) later suggested that they tend to be found in water logged depressions. Within the study area at Fongoli neither of these attributes was used as criteria. Rather "grasslands" represented more open stretches (similar to plateau), although characterized by <10% woody plant covering (Lawesson, 1995). Lawesson (1995), in censusing and characterizing the flora composition and density of Sénégal, described numerous types of "grasslands" (e.g. desert grassland, semi-desert grassland, etc.). The current project will use only his distinction of grasslands from "wooded grasslands," with the latter known to be 10-40% covered by woody plants. Like in Western Tanzania, these areas typically cover the plateaus during the wet season (Kano, 1971), however, often have widely distributed pockets of woody shrubs. These areas closely resemble "plateau" during the late dry season when fires unreservedly burn across the entire region. In the wet season, however, all grasslands typically contain monospecific stands (Hunt & McGrew, 2002).

Woodland (Figures 4.6., 4.7.)

"Woodland" is perhaps the most common habitat type found across the African continent and yet the word has no common reference, i.e. no single definition is yet able to simultaneously account for canopy cover, density, dominant species, etc. across all habitats. This ambiguity is exaggerated by area that are dominated by single-species trees that do not exist in similar densities at other sites [e.g. *Pterocarpus* in Sénégal (McGrew et al., 1981; Pruetz et al., 2002; pers. obs.), *Brachystegia* in Tanzania (Kano, 1971, 1972; Nishida, 1989; Moore, 1992)]. The high rate of variation seen in all of these and other features typically demands researchers elaborate on particular habitat types within their study site. No more clearly is this seen than in savanna woodlands, where numerous different types have been described – open, closed, bushland, transition, medium density, shrubland, etc. – that make up an ecological gradient with no truly known endpoints (Aubreville, 1950; Ellenberg and Mueller-Dombois, 1967; Lawesson, 1995).

Unfortunately, though, what characterize the Fongoli region best are the deciduous woodlands that cover the majority of the terrain within the study area (Lawesson, 1995; pers. obs.). Although this type of habitat was thought to cover <37% of the study site in Mt. Assirik (Tutin et al., 1983), it is predicted to cover a significantly higher proportion of the

Fongoli site. Deviating from Hunt and McGrew's (2002:38) claim that woodlands typically occur in "well drained slopes and valleys," woodlands in Fongoli show no apparent relationship with topography and blanket wet and dry landscapes. They are distinguished from gallery forests by their lower density of tree distribution, lower diversity of tree species, and smaller canopy cover (Lawesson, 1995). It is, however, a very widespread vegetation type, found ubiquitously throughout Western Mali (Duvall, 2001), Guinea (Aubreville, 1950) and Sénégal (Kédougou specifically – Adam, 1965; Lawesson, 1995).

Figure 4.6. and 4.7. Examples of savanna woodlands, which covers much of the study area, during late dry (left) and wet seasons in Fongoli, Sénégal. Notice the distance between canopy tops; chimpanzees are therefore forced to move terrestrially in these habitats.

Bamboo

The final habitat type described here is bamboo thicket. Following Ellenberg and Mueller-Dombois' (1967) description, Baldwin et al. (1982:370) considered this habitat as "flat-leaved savannas with isolated palms and deciduous trees." Few such palms remain in the Fongoli study area and so this area was characterized as having thickets or walls of bamboo (both alive and dead) that were found in small patches, usually dispersed widely in grasslands. Bamboo remains a source of food for chimpanzees in a community of chimpanzees in Baffing Reserve, Mali (pers. obs; Duvall, pers. comm.), although only rarely has evidence of bamboo consumption been observed in the Fongoli community (Pruetz, pers. comm.). During the current study, chimpanzees were seen traveling through this habitat-type, but never resting or feeding in it.

4.3 Results

In total, 75 different individual feeding trees of 18 species were identified and sampled (Table 4.1.). A sample size of 10 individuals per known feeding tree species was examined. If this criterion could not be met with marked feeding trees additional feeding-species trees that fell within two predetermined transects were used. This limited the number of trees used in analysis to six (see Table 4.3). The PCQ method (Figure 4.8.) was slightly

TABLE 4.1. Each of the 18 different known feeding species and the number of individual trees marked within the study area

Species	**# of marked feeding trees**
Ficus spp.	14
Adansonia digitata	10
Pterocarpus erinaceus	6
Baissea multiflora	5
Landolphia heudelotii	5
Saba senegalensis	5
Spondias monbin	5
Cola cordifolia	4
Petit Minkone (local name)	4
Parkia biglobosa	3
Dehe Dehe (local name)	2
Hexalobus monopetalus	2
Piliostigma thonniagii	2
Lannea microcarpa	1
Khaya spp.	1
Masarikeno (local name)	1
Acacia ehrenbergiana	1
Diaspyros mespiliformis	1

modified and used to determine the average distance from the marked tree to the four closest individuals of the same species. From this the average distance could be calculated and,

Fig. 4.8. Researcher measuring the distance between feeding tree species (habitat - woodland, dry season)

following Barbour et al. (1999), the density of that species/hectare could be found. Table 4.2 shows these different densities for six common feeding species for the Fongoli community. *Baissea multiflora* was found to be the most common of the known feeding species with baobob trees (*Adansonia digitata)* (see Chapter Five, Figure 5.14.) the rarest. Although data on feeding tree distribution are not available from savanna chimpanzee sites, it is thought that a higher density of trees, in general, provides increased potential food sources and sleeping sites (Moore, 1992).

Discussion

For how these widely distributed food sources are thought to influence Fongoli chimpanzee grouping behavior, see Discussion sections in Chapters Five and Six.

TABLE 4.2. Six common feeding tree species, average distance to nearest neighbor, and estimated density within the Fongoli community

Tree Species	Mean distance, nearest neighbor	Density (trees/100 km^2)
Ficus spp.	22.8	438.77
Saba senegalensis	28.8	347.17
Pterocarpus erinaceus	20.8	479.74
Adansonia digitata	67.2	148.84
Hexolobus monopetalus	16.9	591.84
Baissea multiflora	12.3	814.33

Sources

Adam JG. 1965. Generalites sur la flore et la vegetations du *Sénégal. Etudes Sénégalaises,* 9:155-214.

Aubreville A. 1950. Flore forestsiere soudano-guinéenne: AOF-Cameroun-AEF. Paris, Soc. Editions Géographiques, Maritimes et Coloniales.

Barbour MG, Burk JH, Pitts WD, Gilliam FS, Schwartz MW. 1999. *Terrestrial Plant Ecology*. Menlo Park: Addison Wesley Longman.

Baldwin PJ. 1979. The natural history of the chimpanzee *(Pan troglodytes verus)* at Mt. Assirik, *Sénégal.* Unpublished Ph.D. thesis, Stirling: University of Stirling.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *International J of Primatol* 3(4):367-385

Boesch C. 2002. Cooperative hunting roles among Tai chimpanzees. *Human Nature-Int Bios* 13(1):27-46.

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Clavette K. 2003.Conservation through Folklore: Ethnoprimatology in Southeastern Sénégal. Unpublished MA Thesis: Northern Arizona University.

Cottam G, Curtis JT. 1956. The Use of Distance Measures in Phytosociological Sampling. *Ecology* 37(3):451-460.

Dart R. 1925. *Autraliapithecus africanus,* the man-ape of South Africa. *Nature* 115:195-199.

Duvall CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21(4):173-203.

Duvall CS. 2001. Habitat, conservation, and use of *Gilletiodendron glandulosum* (Fabacae, Caesalpinoideae) in southwestern Mali. *Syst Geogr* 71:699-737.

Ellenberg H, Mueller-Dombois D. 1967. Tentative physiognomic-ecological classification of plant formation of the earth. *Berichte de Geobotanischen Institutes der Eidgenossischen Technische Hochschule Stiftung Rubel* 37:21-46.

Frederiksen P, Lawesson JE. 1992. Vegetation types and patterns in Sénégal based on multivariate-analysis of field and NOAA-A VHRR Satellite Data. *J of Veg Scienc* 3(4):535-544.

Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: The Belknap Press of Harvard University.

Harrison MJ. 1983. Age and Sex Differences in the Diet and Feeding Strategies of the Green Monkey *Cercopithecus sabaeus. Animal Behaviour* 31(4):969-977.

Hunt KD. 1994. The evolution of human bipedality: ecology and functional morphology. *J of Human Evolution* 26:183-202.

Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Mont Assirik, Sénégal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 35-51.

Kano T. 1971.The chimpanzees of Filabanga, Western Tanzania. *Primates* 12:229-246.

Knutsen PG. 2003. Threatened existence: *Saba Sénégalensis* in southeastern *Sénégal.* Unpublished MA thesis, Ames: Iowa State University.

Lawesson LE. 1995. *Studies of woody flora and vegetation in Sénégal.* Copenhagen: Council for Nordic Publications in Botany.

Marchesi P, Marchesi N, Fruth B, Boesch C. 1995. Census and distribution of chimpanzees in Cote d'Ivoire. *Primates* 36(4):591-607.

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirk, Sénégal, West Africa. *J of Human Evolution* 10:227-244.

McGrew WC, Baldwin PJ, Tutin CEG. 1988. Diet of wild chimpanzees *Pan troglodytes verus)* at Mt. Assirik, *Sénégal*: I. Composition. *Am, J. of Primatol* 16:213-226.

Mitani JC, Watts DP. 1999 Demographic influences on the hunting behavior of chimpanzees. *American J of Phys Anthropol* 109(4):439-454.

Moore J. 1992. 'Savanna chimpanzees'. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 99-118.

Naughton-Treves L, Mena JL, Treves A, Alvarez N, Radeloff VC. 2003.Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Cons Biol* 17(4):1106-1117.

Nishida T. 1989. A note on the chimpanzee ecology of the Ugalla Area, Tanzania. *Primates* 30(1):129-138.

Pruetz JD. 2002. Competition between savanna chimpanzees and humans in southeastern Sénégal. *Amer J Phys Anthropol* 128-128 Suppl. 34 2002

Pruetz JD, Knutsen P. 2003. Scrambling for a common resource: Chimpanzees, humans, and *Saba Sénégalensis*, in southeastern Sénégal. *Amer J Phys Anthropol* 172-172 Suppl. 36

Pruetz JD, Marchant LF, Arnot J, McGrew WC. 2002. Survey of chimpanzees *(Pan troglodytes verus)* in southeastern Sénégal. *Amer J of Primatol* 58:35-43.

Reed KE. 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. *J of Human Evolution* 32(2-3):289-322.

Sall M. 2000. *Atlas du Sénégal.* Paris: Les Editions J.A.

Sharman MJ. 1981. Feeding, Ranging and Social Organization of the Guinea Baboon. Ph.D. diss., Scotland: University of St. Andrews.

Stanford CB. 1995. The influence of chimpanzee predation on group-size and antipredator behavior in red colobus monkeys. *Animal Behaviour* 49(3):577-587.

Stanford CB. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey.* Cambridge, Ma: Harvard University Press.

Stanford CB. 1999. *The Hunting Apes: Meat-eating and the Origins of Human Behavior.* Princeton, New Jersey: Princeton University Press.

Stanley SM. 1992. An ecological theory for the origin of *Homo Paleobiology* 18:237-257.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

White F.1983. *The vegetation of Africa. A descriptive memoir to accompany the Unesco/AETFAT/UNSO vegetation map of Africa.* Unesco, Paris.

Wrangham RW. 1999. Evolution of coalitionary killing. *Yearbook of Phys Anthropol* 42:1-30.

Chapter Five: Daily party size

5.1 Introduction

What is in a party?

Those who study primates have long been interested in the factors influencing the gregariousness that characterizes the Order (Wrangham, 1980; van Schaik 1983, 1989; Janson & Goldmsith, 1995; Treves and Chapman, 1996; Sterk et al., 1997; Pepper et al., 1999; Chapman and Chapman, 2000). Initial indications are that variables such as resource availability and predation may affect primate grouping differently (a) in various habitats and (b) between the sexes. For example, food availability, distribution, and quality are thought to affect females more than males just as animals living in moist, tropical rainforests are thought to be less sensitive to these variables than those individuals living in drier, more open conditions. In attempting to examine the effect that ecology has on social behavior, studies have often centered their foci on the philopatric sex, trying to understand how core resident animals influence the behavior of a social unit. In chimpanzees *(Pan troglodytes)*, though, conflict remains as to what influence each sex has on the dynamics of a community. For example, whereas some work has found males to be significantly more social and influential in grouping patterns (Reynolds and Reynolds, 1965; Goodall, 1986; Wrangham, 2000), others have concluded that males and females are equally gregarious (Sugiyama and Koman, 1979; Ghiglieri, 1984), thus blurring the social nature of each sex and the community as a single unit. Furthermore, other factors that influence grouping behavior, such as infanticide avoidance and feeding competition, may simultaneously affect the overall dynamics of any particular group's social organization (see Chapter Two).

Because of the fluid, fission-fusion nature of chimpanzee sociality the proximate factors that determine which animals aggregate together and for how long has been studied at many sites. Most studies have focused on food abundance and the effect of estrous females, tending to conclude that both are reliable predictors of chimpanzee party size (Chapman et al., 1995; Doran, 1997; Pepper et al., 1999; although see Newton-Fisher et al., 2000). Differences in food abundance, however, do not account for all the variation we see in

grouping patterns (Wrangham et al., 1993, 1998; Chapman et al., 1994, 1995; Mitani et al., 2002) and so researchers have turned to other likely variables, including those that are demographic (Sakura, 1994) or social (Goodall, 1986; Matsumota-Oda et al., 1998; Mitani and Watts, 1999; Newton-Fisher, 1999; Pepper et al., 1999; Boesch & Boesch-Achermann, 2000; Hashimoto et al., 2001;), in order to better understand influencing factors.

Defining Party and the effect of habitat

Variation in ecological structure and composition of chimpanzee habitat types often cause researchers to operationally define 'party' for each study (Chapter One, Table 1.1.). These definitions have proved inconsistent and therefore problematic, especially as criteria have been shown to vary within and among study sites as well as over time. This variation may have caused some of the discrepancies reported for observed party sizes (Table 5.2.; see also Chapman et al., 1993). Moreover, "simply defining a party presents problems since chimpanzees sometimes disperse over a wide area yet move together in a single direction in an amoeba-like fashion" (Pepper et al., 1999:618). Given this inconsistentcy, the current study sought to apply multiple definitions to a given party in the attempt of assessing inter-definition reliability.

In areas that offer a mosaic of habitats (such as Fongoli), it is thought that chimpanzees will exhibit grouping patterns not seen in communities living in more uniform environment (see Chapter Three). Two examples support this. The first comes from Mt. Assirk, Sénégal, where Tutin et al. (1983) found that chimpanzee parties were larger in open areas, whereas smaller parties, particularly mother-offspring parties, were found to avoid these areas, probably because they are more vulnerable to predators.[1] The second example was reported from Bossou, Guinea, were chimpanzees inhabit mostly primary and secondary forest surrounded by savanna and gallery forest corridors (Takemoto, 2004). Takemoto (2004) found that chimpanzees there spend more time in trees during the rainy season than in the dry season, thereby reducing thermoregulation costs and benefiting from the

[1] Boesch (1991), in a study of leopard predation on chimpanzees in Tai Forest, Ivory Coast, suggested that the increased risk open areas provide for prey would be "nullified" by the increased visibility such allows – see "Predation Pressure", this chapter.

microclimate of the canopy. Only at study sites where relatively greater habitat variation exists (i.e. savanna/mosaic regions) can patterns like these emerge. Extreme seasonality in core areas may demand these populations adopt measures that are unnecessary for forest-dwelling chimpanzees. As Moore (1992:108) suggests, what is being seen here can be described as a

> "'savanna chimpanzee adaptation' of larger, more stable, mixed sex groups that nomadically exploit resources distributed patchily within a large home range – an image of obvious relevance to hominid origin models."

In some ways, then, chimpanzee social behavior and party size specifically, may be indicative of the habitat in which these apes live.

TABLE 5.1. To estimate community size researchers often extrapolate from the largest observed party size.

Site	% of Community	Source
Bossou	100	Sugiyama and Koman, 1979
Budongo	81	Suzuki, 1969
Budongo	60	Sugiyama, 1981
Gombe	64	Teleki, 1973
Tai	81	Boesch, 1991

Besides habitat, community size can also be extrapolated through the size of subgroupings. Whereas some have used food distribution and density to estimate chimpanzee density (see Balcomb et al., 2000), the maximum size of an observed party often predicts well the total number of individuals in a community. Tables 5.1. shows the largest known party size in five different studies. Using this value, the largest day party observed during the current study (21, see Table 5.2.) would conservatively suggest a community size at Fongoli of 27 individuals.

Table 5.2: Mean party sizes of chimpanzees and corresponding community estimates (denotes community estimates not available)*

Community Name	Site	Mean Party Size	Estimated Community Size	Source
Budongo	Budongo, Uganda	3.9		Reynolds & Reynolds, 1965
Budongo	Budongo, Uganda	4.4	50	Sugiyama, 1968
Gombe	Gombe, Tanzania	4.0	60	Goodall, 1968
Mahale	Mahale, Tanzania	6.2	29	Nishida, 1968
Rio Muni	Okorobiko Mtns, Rio Muni	9.9	>23	Sabater Pi, 1979
Bossou	Bossou, Guinea	8.7	NA	Sugiyama & Koman, 1979
Bossou	Bossou, Guinea	6.0	20	Sugiyama, 1981
Assirik	Mt. Assirik, Sénégal	4.6	25	Baldwin, 1979
Ngogo	Kibale, Uganda	2.6	55	Ghiglieri, 1984
Gombe	Gombe, Tanzania	4-5	51	Goodall, 1986
Kanyawara	Kibale, Uganda	5.6, 6.1	NA	Wrangham et al., 1992
Kanyawara	Kibale, Uganda	5.1	27	Chapman et al., 1994
Tai	Tai Forest, Ivory Cst	3.45	70	Doran, 1997
Tai	Tai Forest, Ivory Cst	10.1	76	Boesch & Boesch-Achermann, 2000
Sonso	Budongo, Uganda	5.7	46	Newton-Fisher, 1999; 2003
Ngogo	Kibale, Uganda	10.27	150	Mitani et al., 2002
Goualougo	Goualougo, DRC	3.22	>14	Morgan & Sanz, 2003
Fongoli	Sénégal	4.1	27	Current study

5.2 Predicting Party size in Pan

Compared with fixed-sized groups, fission-fusion social systems allow more flexibility in that individuals decide where they travel and with whom. It has been shown that *Pan* and *Ateles* do adjust grouping behavior to various ecological and social variables (*Pan:*

see below; *Ateles:* Symington, 1987; McDaniel, 1994). Chimpanzees and other primates, then, inevitably arrive at a point where feeding in smaller groups is ultimately more advantageous than feeding in larger ones due to the costs incurred by increased aggression and travel time while in large parties (Wrangham et al., 1992; Chapman et al., 1995; Chapman and Chapman, 2000). Goodall (1986) first suggested that female sexual receptivity was the single most important influence on party size and social organization in chimpanzees. Other factors are, however, influential. Larger parties have been observed when chimpanzees hunt (Boesch & Boesch-Achermann, 2000), when predation pressures are high (Boesch, 1991; Sakura, 1994) and when traveling (Tutin et al., 1983). Fluctuations in the size and quality of food patches, party location, and party activity have also contributed to party-size changes (Goodall, 1986; White & Wrangham, 1988; Anderson et al., 2002; Hashimoto et al., 2003). Most importantly, though, the size of these groups does consistently positively correlate with the number of estrous females in a party (Goodall, 1986; Sakura, 1994; Doran, 1997; Matsumoto-Oda et al., 1998; Matsumoto-Oda, 1999; Hashimoto et al., 2001; Mitani et al., 2002;) with larger parties typically staying together longer (Wrangham et al., 1992; Boesch & Boesch-Achermann, 2000 - Fig. 5.1.).

There are costs and benefits to aggregating in large parties. An increase in group size may indicate increased within group competition (WGC) for food sources (Wrangham, 1980; Sterk et al., 1997), especially when foods are more patchily distributed (Isbell, 1991). Moreover, large groups have long thought to have evolved, not as a means of reducing feeding competition (Wrangham, 1980), but rather because they reduce predation vulnerability (van Schaik, 1983, 1989; Janson and Goldsmith, 1995). Despite the apparent benefits to forming large parties, however, there exist disadvantages as well. In chimpanzees males in large parties have longer daily ranges than solitary ones and both sexes spend less time feeding when they are in large parties (Wrangham, 1977; Wrangham and Smuts, 1980; Mitani et al., 2001; Matsumoda-Oda, 2002). Moreover, aggression for food and mates is significantly greater in larger parties than in smaller ones (Wrangham, 1980; Goodall, 1986; Wrangham et al., 1993). Finally, costs of travel increase proportionally due to the greater distances large parties must travel to meet nutritional and energy demands (Isbell, 1991; Chapman et al., 1995; Janson and Goldsmith, 1995). In sum, predicting party size in

chimpanzees must take into considerable numerous variables, most importantly estrous female presence and food abundance/distribution (see below).

Estrous females

Sexually receptive female chimpanzees who are not forced into consortships by dominant males will almost certainly find themselves surrounded by most of the community during their peak swelling days. Males use aggression and coercion to solicit a receptive female. At Gombe, Goodall (1986) observed one female to copulate 84 times over an eight day period with seven different males within her community. During that same time span, 169 aggressive encounters were seen, more than twice the normal rate. The reproductive opportunity an estrous female presents to males causes large parties to form whenever females reach this peak period of ovulation. Examination, however, of how estrous females influence mean party size often results in an analysis not of overall party size, but of the number of males within a party. Anestrous females typically join these large aggregations, but not always, and females with young infants are even less likely to expose their vulnerable offspring to periods of increased aggression. Because in some studies there is no relationship between the number of males and the number of anestrous females within parties (Hashimoto et al., 2001), the latter group is often not considered a factor. The above distinction, however, underlies a deeper problem: That of how to reliably assess the variables acting independently on group size. Although the number of males increases with the number of estrous females, one does not necessarily respond to the other. Statistical analyses can eliminate other possible factors (see Hashimoto et al., 2001), but a better understanding of movements of individual chimpanzees within a community is needed to grasp how the dynamics of social grouping manifest themselves.

Resource abundance

At most sites chimpanzee party size has been observed to vary with fruit availability (Goodall, 1986; Doran, 1997; Matsumoda-Oda et al., 1998; Boesch and Boesch-Achermann, 2000; Hashimoto et al., 2001; although see Newton-Fisher et al., 2000; Hashimoto et al., 2003). Mean chimpanzee party size is predicted to increase as the distance traveled between

food sources decreases. Larger parties have become so renowned that some researchers have begun to use the term "core" party during these fruit-rich periods, a word describing a party with most of the adult males within a community (Wrangham et al., 1992). Similar core parties have been seen at Budongo (Sonso community: Newton-Fisher, 2000), Gombe (Goodall, 1986), Mahale (Nishida, 1968), and Tai (Boesch & Boesch-Achermann, 2000), and are thought to also exist in savanna communities.

While some unequivocally maintain that food abundance constrains party size (Wrangham et al., 1992; Boesch, 1996; Wrangham, 2000), others contend that food abundance affects sexes differently. For example, it has been suggested that male aggregation patterns respond more to social factors than ecological ones, i.e. to gain or increase sexual or political advantages over conspecifics (Wrangham & Smuts, 1980; Newton-Fisher, 1999). This idea was supported at Mahale, Tanzania where researchers found no relationship between the number of males in a party and fruit abundance. (Hashimoto et al., 2001, 2003). Similarly, within the Sonso community of chimpanzees of Budongo Forest, Uganda, parties exhibited either a negative or no relationship with fruit abundance. The authors suggested that, rather than form large parties during fruit-rich periods, these chimpanzees were observed to disperse and utilize more, but smaller, patches rather than aggregate at single, large ones (Newton-Fisher et al., 2000). Similarly, Sakura (1994), after comparing party sizes across sites, concluded that ecological factors may play a very small role in chimpanzee party size formation and that other (social) explanations are needed to explain what determines grouping patterns. No known data are available on savanna chimpanzee party size in response to resource abundance, though Izawa (1970) did suggest that at Kasakati, parties[2] spent more time together when foods were scarce. Whether the author was referring to food abundance or distribution is not clear as no systematic behavioral or ecological data were collected.

Predation Pressure

A final factor that has been shown to affect party size in chimpanzees is predation pressure. Although they are large bodied, even adult chimpanzees are vulnerable to attacks

[2] Izawa (1970:17) called them "temporary groups" after Goodall (1965)

by predators. Boesch (1991), measuring the effects of high and low predation pressure during food-rich and poor seasons at Tai National Park, Ivory Coast, found that, during food-rich periods, party size decreased when predation pressure increased. The effect was not universal, however, with all male and mixed parties varying the most. This suggests that predation pressure is party-type specific. Boesch, however, concluded that the two factors (food availability and predation pressure) generally "nullify" each other, arguing that food availability does contribute to changes in both party size and type, although in times of shortage, predation pressure will constrain the variability of both.

The only other available data on predation pressure are from Bossou, Guinea, where Sakura (1994) examined the change in party size when a community there was forced to cross a paved road that bisected their home range. Although few cars use the road, vehicle traffic was thought to present a possible danger for the chimpanzees. No change in party size was found, however, when chimpanzees approached or crossed the road. It seems likely that where predators exist in high densities, their impact on chimpanzee grouping behavior will be more clear, perhaps working as a major influence on its dynamics. The only available data of predation pressure on savanna chimpanzees was reported from Mt. Assirik, Sénégal. Despite living in a habitat that provides increased visibility and likely low predator densities, reports from the Assirik studies of the 1970s suggest that these chimpanzees may form larger parties for traveling, perhaps in response to predation pressure (Tutin et al., 1983). Lion *(Panthera leo),* leopard *(P. pardius),* spotted hyena *(Crocuta crocuta),* and the African hunting dog *(Lyacon pictus)* all live with the Assirik community within the PNNK (Baldwin et al., 1982). Even with increased visibility in this type of savanna habitat, less opportunity for escape (i.e. low large tree density) may increase the effect of predators on grouping behavior.

5.3 Methods

The current study focused on the Fongoli community of chimpanzees in southeastern Sénégal (12°55'N 16°02'W). This region has been characterized as a Sudanian-Guinean mosaic habitat, composed mainly of woodland-savanna, and broken up by large stretches of lunar plateau and pockets of gallery forest (Hunt and McGrew, 2002; McGrew et al., 1981). The village of Fongoli (Figure 5.5.) lies between 6 and 10 km NW of the regional capital of Kédougou and <50 km SE of the Parc National du Niokolo Koba (PNNK), not far from the Malian (~ 85 km) or Guinean (~35 km) borders. Permission to conduct research in the area has been granted to Jill Pruetz by the Department du Eaux et Forets du Sénégal, as well as by local tribal leaders of the surrounding villages.

Study Site

The study area itself is a 63 km^2 region and contains four villages: the smallest (Fongoli) being home to <50 people and the largest (Djendji) <500 (pers. obs.). Between these villages much of the land is heavily disturbed by people from the encompassing villages and also those from Kédougou (Figure 5.11.), who have established agricultural fields throughout the area (Knutsen, 2003). Because the study period was limited to seven months, if and how often chimpanzees use uninhabited crop fields and whether party size was adjusted because of that could not be assessed. It is thought, however, that all animals typically avoid these rather open areas for the same reasons they avoid plateaus (predation and heat). Human presence is seen throughout the area during all months. Most hunters await potential game at valued water sources and appear to prefer warthog *(Phacochoerus aethiopicus)* and monkey *(Cercopithecus aethiops* and *Erythocebus patas)*, avoiding chimpanzee in response to cultural traditions (Clavette, 2003). Overall resource competition between humans and nonhumans is thought to be highest during late dry seasons when food and water availability are predictably low for all organisms (Duvall, 2000; Pruetz, 2002).

Study Subjects

Study subjects (Figure 5.1.) were individuals in the not yet fully-habituated, non-provisioned Fongoli community of chimpanzees in southeastern Sénégal. At the end of the current study, in December 2003, 16 adult individuals had been identified (10 males and 6 females). Combined with a largest single party observation of 22 individuals, Pruetz (unpublished data) has estimated a minimum community size of 27 individuals. Most chimpanzee encounters resulted in multiple contacts with a single party for a variable amount of time, although single sightings were not infrequent. For the current study, average distance from observer to chimpanzee party ranged from 10 meters to over 100 (N=67).

Fig. 5.1. One of the adult males at Fongoli

Flora and Fauna at Fongoli

Flora

For a discussion of the flora at Fongoli, see Chapter Four.

Fauna

Whereas the earlier SAPP was conducted within the boundaries of the PNNK, the current study examined a chimpanzee population living sympatrically with humans outside the Parc. Despite high numbers of potential chimpanzee predators surveyed within the PNNK (see Baldwin et al., 1982; Pruetz et al., 2002), evidence suggests that most large

predators at the Fongoli study site have been extirpated by local hunters (pers. obs.)[3, 4], not necessarily as a response to crop loss incurred by these animals (Naughten-Treves et al., 2003), but rather to provide supplemental nutrition for farmers. Even with minimal hunting pressure, however, it is unlikely that most species in this region, especially within the Order Primates, can sustain additional survival threats with increased human population (Sall, 2000) and expanding agricultural practices (Knutsen, 2003) already decimating current populations (pers. obs).

Prey and unlikely hunting behavior

At other study sites chimpanzees have been observed to prey on a variety of mammalian species, including members of the orders Primates, Rodentia, and Carnivora among others. (Goodall, 1986, Table 11.1, 11.2; Stanford, 1999). Moreover, at Gombe National Park, Tanzania, chimpanzee hunting is thought to significantly influence population dynamics of neighboring groups of red colobus monkeys (Stanford, 1998, 1999). At Gombe and other communities such as Ngogo, Uganda (Mitani and Watts, 1999), Kanyawara, Uganda (Wrangham, 1999), or Tai, Ivory Coast (Boesch and Boesch-Achermann, 2000; Boesch, 2002) where hunting is seen often, chimpanzees cooperate to trap monkeys in high-story canopies where prey eventually are forced to take high risk chances to avoid capture (Stanford, 1995, 1998; Boesch, 2002). This scenario, however, would be logistically impossible at Fongoli where tiny pockets of gallery forest make up only a very small proportion of the total area. In fact, only rarely have chimpanzees been seen moving from tree to tree without first having to descend (pers. obs.). Hunting strategies like the one mentioned above, then, are not expected at Fongoli or any other savanna site for three reasons. The openness and dryness of the habitat are likely to forewarn potential prey of chimpanzee presence, therefore allowing amble time to avoid possible male hunting parties (Mitani and Watts, 1999; Boesch, 2002). Second, in these habitats most of the potential prey animals are terrestrial (save for bushbabies) and thought to be quicker than chimpanzees (i.e. easily able to elude them) if a chase did occur. Finally, although no one has yet

[3] The remains of a discovered chimpanzee carcass suggest the possible killing by a leopard *(Pantera pardus)*, although it has been many years since anyone has observed one.
[4] Local people from around the study area claim hyenas still exist in small numbers, although no evidence of their presence has yet been found by researchers (Stewart, pers. comm.).

systematically explored savanna chimpanzee hunting behavior, it is thought to be energetically inefficient during much of the year when food and water sources are not abundant. What evidence does exist for meat eating is thought to an artifact of opportunistic and energetically inexpensive captures of smaller mammals (Pruetz, pers. comm.).

Following Baldwin (1979), Table 5.3. lists other wildlife in the area and their relationship to chimpanzees. Other than other diurnal primates who will compete for high quality fruits (Kano, 1971; Sharman, 1981; Harrison, 1983), most large mammals are not thought to compete with chimpanzees for food sources, although all animals are predicted to compete heavily for water sources during the dry season.

Table 5.3. List of all known primates and small mammals observed at Fongoli during the study period

Scientific Name	Common Name	Relationship to Chimpanzee
Papio hamadryas papio	Guinea baboon	Competitor
Cercopithecus aethiops	Green monkey	Competitor; Prey?
Erythrocebus patas	Patas monkey	Competitor
Galago senegalensis	Senegalese bushbaby	Prey
Mungus mungo	Banded mongoose	none
Hystrix crisatta senegalica	Crested porcupine	none
Viverra civetta	African civet	none
Genetta genetta	Common genet	none
Felis sylvestros libyca	African wild cat	none
Helioscirius gambianus	Gambian sun squirrel	Potential prey?
Xerus erythropus	Striped ground squirrel	Potential prey?
Phacochoreus aethiopicus	Warthog	none

Previous Chimpanzee Research in Sénégal

The last formal chimpanzee study began in Sénégal 1976 with the initiation of the Stirling African Primate Project (SAPP). Beginning a long-term research study at Mt. Assirik, in the PNNK, the project's objectives included habituation of a community of

Fig. 5.2. Guinea baboons *(Papio p. hamadryas)* in the PNNK seen here drinking from a water hole during the late dry season

chimpanzees within the Parc and collection of behavioral and ecological data Baldwin, 1979; McGrew et al., 1981; Tutin (et al., 1983). The project lasted four years with data collected on ranging (Baldwin et al., 1982), diet (McGrew et al., 1988), and social behavior (Tutin et al., 1983); habituation was never fully completed and the project consequently was aborted in 1979.

Efforts to explore savanna chimpanzee socioecology, however, were renewed in this region in 2000 when Pruetz et al. (2002) initiated a survey comparing chimpanzee densities within and outside the PNNK's boundaries. Known as the Miami African Primate Project (MAPP), researchers found that chimpanzee densities had risen within the Parc's boundaries since the SAPP work of the late 1970s. More importantly, results indicated that chimpanzee densities were possibly as high as 0.09 individuals/km^2 outside the Parc (compared to 0.13 individuals/km^2 within the PNNK) where chimpanzees would have to compete with local villagers for scarce water and food sources (Pruetz, 2002; Pruetz et al., 2002; Knutsen, 2003). Densities were lowest in savanna areas (0.008) and highest in gallery forest patches (0.03). Further investigation found that chimpanzees in this region of Sénégal are rarely hunted and co-exist with people of the surrounding villages. As a result of these findings, a long term project was established in 2001 in and around the village of Fongoli, four kilometers south of Kédougou (Figure 5.3.) within the Tomboronkoto region. The project's current objectives are to habituate the Fongoli community while also examining aspects of human-chimpanzee competition for limited resources (Pruetz, 2002; Pruetz & Knutsen, 2002; Knutsen, 2003).

Fig. 5.3. Map of Sénégal, Kédougou is located in the southeast part of the country

Ultimately the project aims to examine the effect of savanna food resources on chimpanzee behavior and social organization.

Data Collection: Locating Chimpanzees

Chimpanzee daily party size and nesting party size were recorded from 22 May – 18 December, 2003. Teams of one to three researchers began each day leaving from Fongoli (Figure 5.5.) or Djendji village around 600-630 and searched for chimpanzees continuously until 200-400 pm. Surveyed areas were determined based on previous days' findings as well as direct and indirect chimpanzee evidence. Most reliable were vocalizations heard during the night, providing approximate areas of nesting sites and direction traveled the following day. Typically these vocalizations were pant hoots, pant barks, or screams (Goodall, 1986), all of which are thought to increase in frequency as party size grows (although see Mitani and Nishida, 1993). As a result of increased vocalizations observed in larger parties, chimpanzee subgroups found via this method (also called "acoustic subgroups," Chapman et al., 1995)

were predicted to be larger than those found using alternative methods (Goodall, 1986; Wrangham et al., 1992).

There were five means of locating chimpanzees. First, discovery of fresh chimpanzee nest groups (see Chapter Six) early in the day allowed researchers to search for chimpanzee trails leaving the area. Second, analyses of chimpanzee feces remains (Chapter Six, Figure 6.6.) also provided insight into their seasonal food preferences and therefore indicated specific areas where parties may be found. Savanna vegetation is thought to be patchily distributed (Bouliere and Hadley, 1970; Lawesson, 1995) and so with the help of local guides, researchers were able to search areas of fruiting trees used seasonally by the Fongoli chimpanzees. Third, during the wet season (June – October) - when plateaus and open grasslands showed signs of vegetation growth – evidence of chimpanzee presence was also found through trails and knuckle prints they left behind while traveling (Figure 5.4.) If researchers found no evidence of chimpanzee presence, (e.g. nests, feces, prints) for

Fig. 5.4. One day old chimpanzee trail left at the end of the dry season (Photo courtesy of F. Stewart).

consecutive days, assistance was sought from local farmers and villages[5] living in the area who often heard chimpanzee vocalizations at night. Finally, during the late dry season, vigils (N=12) were conducted at a permanent water source where chimpanzees aggregate almost daily. When parties were contacted, variables recorded included (a) how the party was

[5] Often times hunters or farmers would observe chimpanzees or hear vocalizations during the late afternoons when researchers were absent. Likewise, if individual chimpanzees slept near villages, people would often hear calls during the night and provide us with information in the morning upon our arrival at Fongoli.

detected, (b) distance from chimpanzees to researcher, (c) type of habitat, (d) number and demographic composition of individuals in party, (e) chimpanzee activity (feeding, traveling, resting), and (f) duration of encounter. Data collection followed Altmann's (1974) all inclusive sampling method.

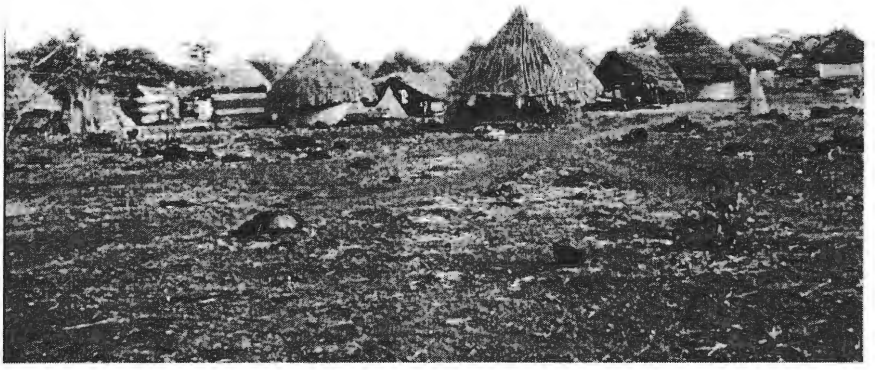


Fig. 5.5. Fongoli village, where researchers began chimpanzee tracking most days

Analyses

Frequency distributions were used to exhibit the range and frequency of daily parties contacted. Student T-tests were used to compare daily party size means under two definitions (one mean including dependent offspring, and one including only adult individuals) and to determine whether there were significant differences in mean party sizes found in different habitats and during different activities. A One-way ANOVA was used to test differences between subgroup sizes detected in different ways.

5.4 Results

Daily Party Size

Of 98 days searching for chimpanzees, parties were seen on 67 occasions. 27 (35.8%) were considered reliable party counts based on Tutin et al.'s (1983) definition (Figure 5.6.). The mean of complete parties encountered was 4.1 (SD = 4.5, N=27; numbers do not include dependent infants or independently mobile juveniles), whereas the mean for all encountered parties was 5.6 (SD = 4.4, N=67). The remaining counts (N=40) are not considered in analyses of party size, party composition, or the impact of estrous females. They are, however, used in analyses examining relationships between party size, habitat, and activity. Chimpanzee party definition followed Tutin et al.'s (1983) one (see Chapter 1, Table 1.1.), although when possible, various definitions were used to assess inter-definition reliability. Specifically, when it was determined that a complete party count had been made, various definitions were applied to a party to examine if the particular definition used by the researcher would affect recorded party count estimations (see Chapter One, Hypothesis # 3). Researchers always attempted to remain with a traveling party, voluntarily aborting an encounter only if individuals within the party appeared stressed by researcher presence; Researchers were sensitive to adult females with young infants and older individuals who struggle more than others to travel under extreme heat. Of the 67 times chimpanzees were encountered, most of these involved multiple contacts within a single observation period; Repeated contacts with a single party have been shown to increase accuracy and count reliability (Wrangham et al., 1992; Pruetz & Leasor, 2002). Most parties were located after they had vocalized (N=40 of 55, 73%). Subgroups detected by vocalization were significantly larger ($F=4.89$, $df=2$, $P<.05$) than those detected by sight.

Role of dependents

Although most studies of party size do not include dependent offspring in their analyses (Sugiyama and Koman, 1979; Wrangham and Smuts, 1980; Sakura, 1994; Mitani et al., 2002), some do (Newton-Fisher et al., 2000), and still others do so only under

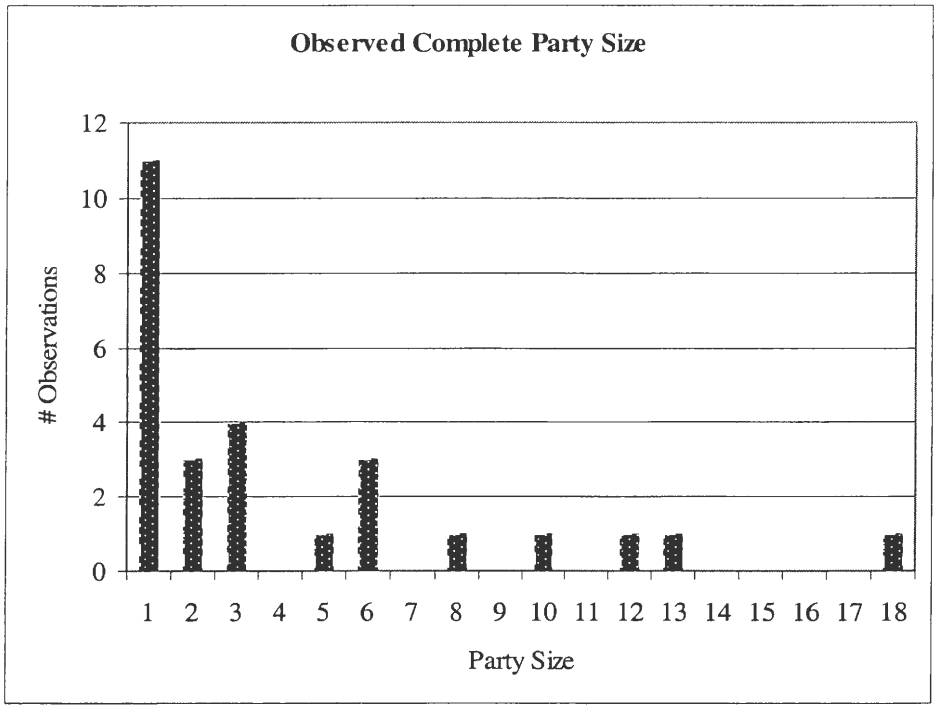


Fig. 5.6. Number of times (N=27) each complete chimpanzee party size was observed throughout the study period

certain conditions (e.g. only when feeding – Hunt and McGrew, 2002). These inconsistencies across studies make inter-site comparisons challenging. Deciding which definition to use often depends upon the aims of the study. For example, in the current study examining the influence of resources on social behavior, young dependent offspring play a critical role in how and to what extent they impose costs on overall grouping dynamics, e.g. resource consumption and traveling (Hrdy, 1999; Ross, 2001). However, further comparison of these data with other sites will not include dependent offspring of any age. Figure 5.7. provides a frequency distribution of all 67 encounters, categorized according to two definitions: one including infants in the final party count (called all inclusive), the other including only independent individuals. Mean party size (MPS) differed significantly when definitions were compared with a paired sample T-test (MPS for adults only: 4.1, all inclusive: 5.7; $p<0.0001$).

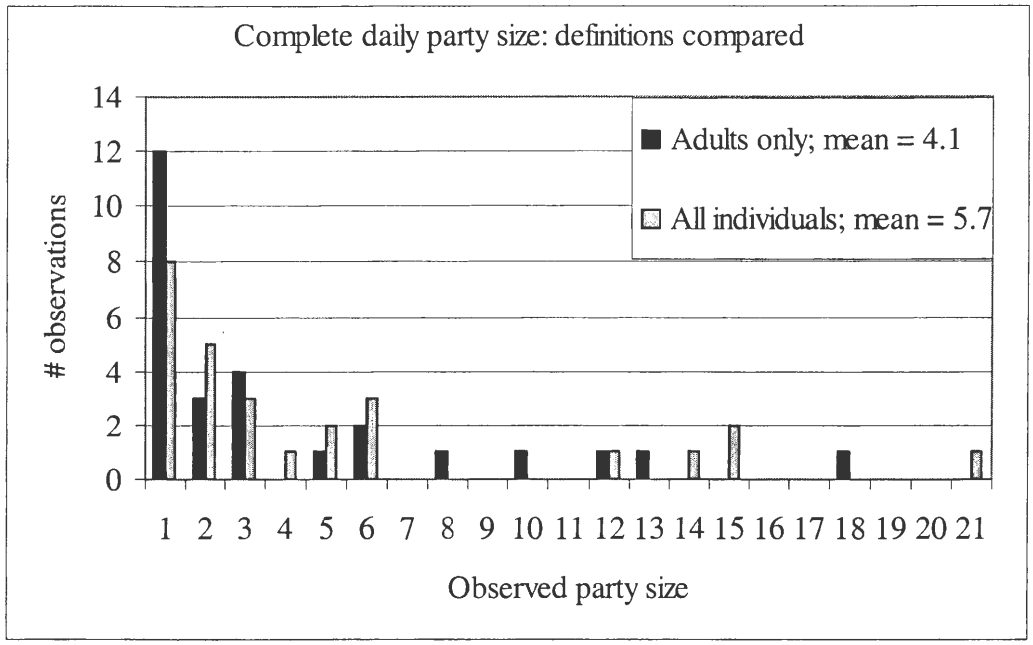


Fig. 5.7. Comparison of observed party size (N=27) results of the Fongoli community between May – December 2003 when infants are included (mean = 5.7) and when they are not (mean = 4.1) in mean party size (MPS).

Comparisons across sites

These data on observed party sizes are compared to other West African study sites in Figure 5.8. Despite differences in habituation levels between Bossou and Fongoli - chimpanzees were provisioned at Bossou (Suguyama and Koman, 1979) - some comparisons can be made. Researches at Bossou defined chimpanzee aggregations in two ways. If chimpanzees were within 30 meters of each other they were considered to be in a "compact association", whereas those individuals >200 meters apart, but still within visual and vocal communication, were considered a 'party' (Sugiyama and Koman, 1979:330). Chimpanzees at Fongoli showed similar patterns of grouping, especially in dry season habitats such as grasslands and open woodlands where visibility was high. The biggest difference between data from Bossou and that of Fongoli was that at Bossou the entire community of chimpanzees was seen together in almost 19% of all observations (Sugiyama and Koman, 1979). The largest party at Fongoli was 21 individuals and at Mt. Assirik it was 22 (Tutin et al., 1983): both thought to be lower than the total community size. Figure 5.9. compares mean party sizes from the two known savanna studies to means from other, forested sites.

Both Fongoli and Mt. Assirik chimpanzees form smaller mean parties than at most other sites, nearly half that of what is observed in the tropical forests of Uganda (Kibale) and Tai (Ivory Coast).

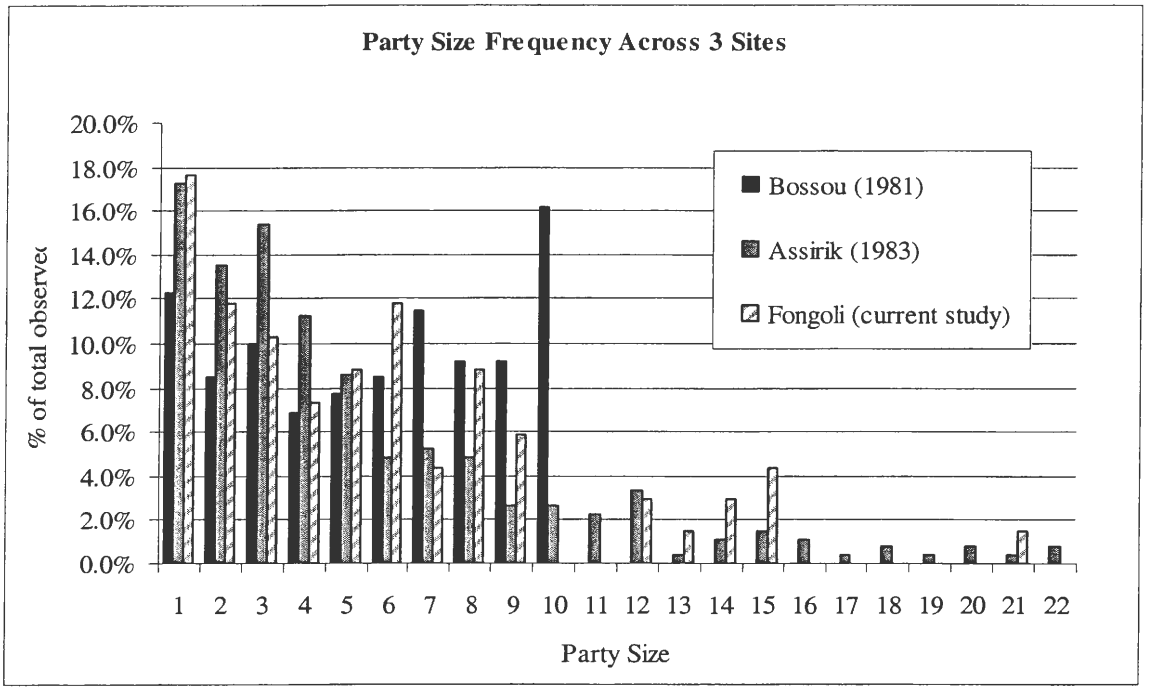


Fig. 5.8. Comparison of party size observed frequency at three West African chimpanzee sites

Detection Method

Detection method did have a significant effect on observed mean party size ($P<.01$). When vocalizations were used, mean party size was found to be 7.1, versus only 2.6 when chimpanzees were found opportunistically. Similar patterns (Figure 5.10.) have also been seen at other, non-savanna sites.

Activity

Results from many studies of forest dwelling chimpanzees suggest that activity patterns correlate with party size. At Tai Forest, Ivory Coast, for example, Anderson et al. (2002) found feeding, resting, and traveling parties to be of similar size and all considerably smaller

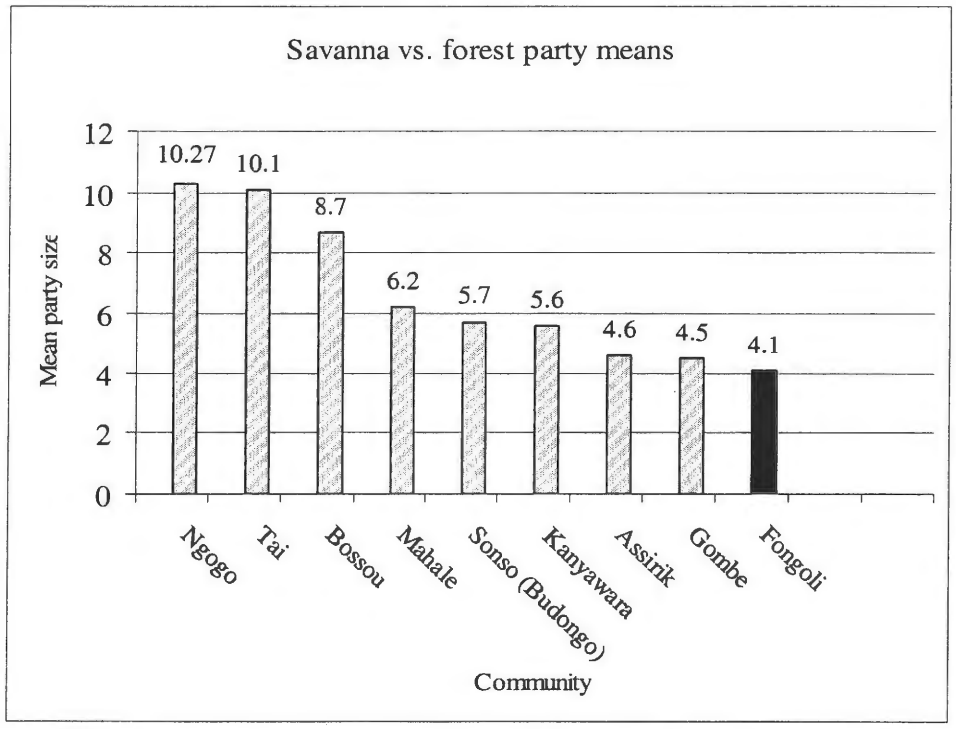


Fig. 5.9. Comparison of means party size between forested and savanna sites

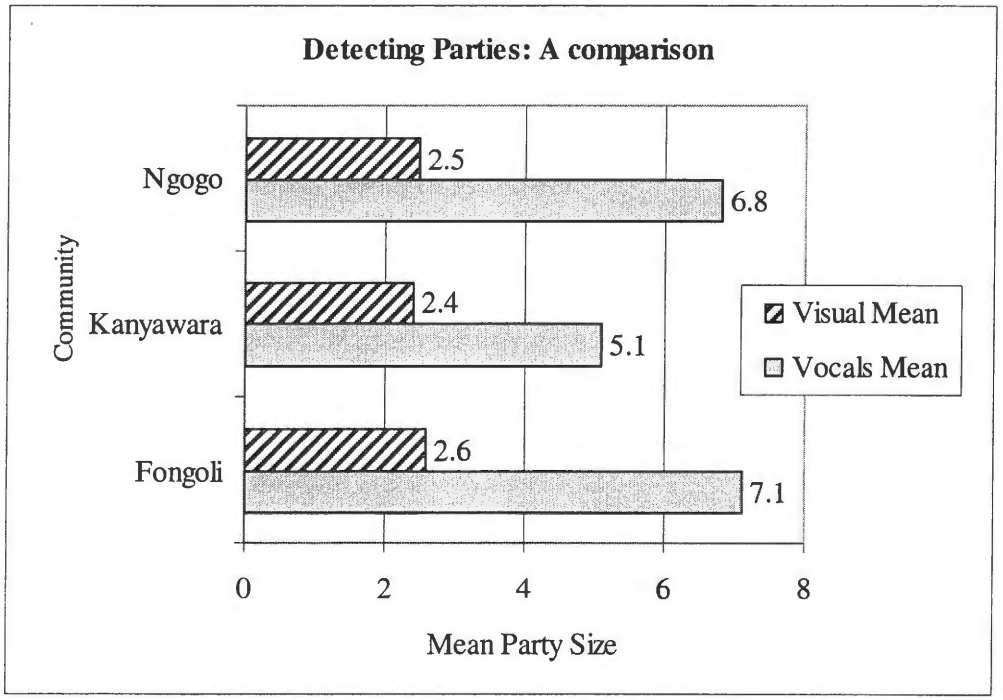


Fig. 5.10. Comparison of two methods used to detect parties at Fongli and two communities in Kibale National Park, Uganda (Kibale data from Wrangham et al., 1992:87)

than meat-eating parties where individuals aggregate for access to a recent kill (see also Goodall, 1986; Mitani and Watts, 1999). It is unlikely, however, that Fongoli chimpanzees consume as much vertebrate prey as those of forested communities. The reasons for this are twofold. First, persistent local hunting has significantly reduced many remaining monkey groups that may otherwise have fallen prey to chimpanzees. As a result, the density of these animals is thought to be lower within the Fongoli community's core range. Second, the potential prey that do remain *(Cercopithecus aethiops, Erythrocebus patas, Papio papio)* are predominantly terrestrial and each have species-specific mechanisms for avoiding capture. These strategies are well suited for savanna habitats where chimpanzee arboreal cooperation (a successful hunting strategy seen in forests) may be extremely difficult. *C. aethiops,* for instance, has been seen to flee into smaller trees unclimbable by larger chimpanzees (Pruetz, pers. obs.), whereas *P. papio* "mob" potential predators (Chapman, 1986) and *E. patas* may be too fast. Therefore, if large parties do not form because of hunting (Goodall, 1986; Boesch and Boesch-Achermann, 1989; Boesch, 2002) at Fongoli, then aggregations of chimpanzees are more likely to be seen in response to something else (Figure 5.11.; Tutin et al., 1983).

Figure 5.11. shows the relationship between mean party size and three activities for all encountered parties: traveling, feeding, and resting (Figure 5.12.). Note in here the inherent partiality towards traveling/fleeing. While some individuals within the Fongoli community seem undisturbed by the arrival of researchers, others remain uneasy and often respond to their arrival by fleeing. Parties engaged in activities *other* than traveling may, upon perceiving researchers, avoid them and therefore when seen, be recorded as 'traveling.' If such is the case, MPS for traveling (5.6, SD=5.3, N=8) would not be accurate and estimates for other activities may be underestimates. Data from feeding parties at Fongoli support this, with mean feeding party size (3.2, SD = 2.8, N=7) observed to be smaller than seen at any other site (see this chapter, Discussion).

Estrus

In all other studies of chimpanzee social behavior, estrous female presence has shown to positively correlate with party size (Goodall, 1986; Wrangham et al., 1992; Sakura, 1994;

Doran, 1997; Matsumoto-Oda et al., 1998; Matsumoto-Oda, 1999; Boesch and Boesch-Achermann, 2000; Hashimoto et al., 2001; Mitani et al., 2002). At Mt. Assirik, in the only

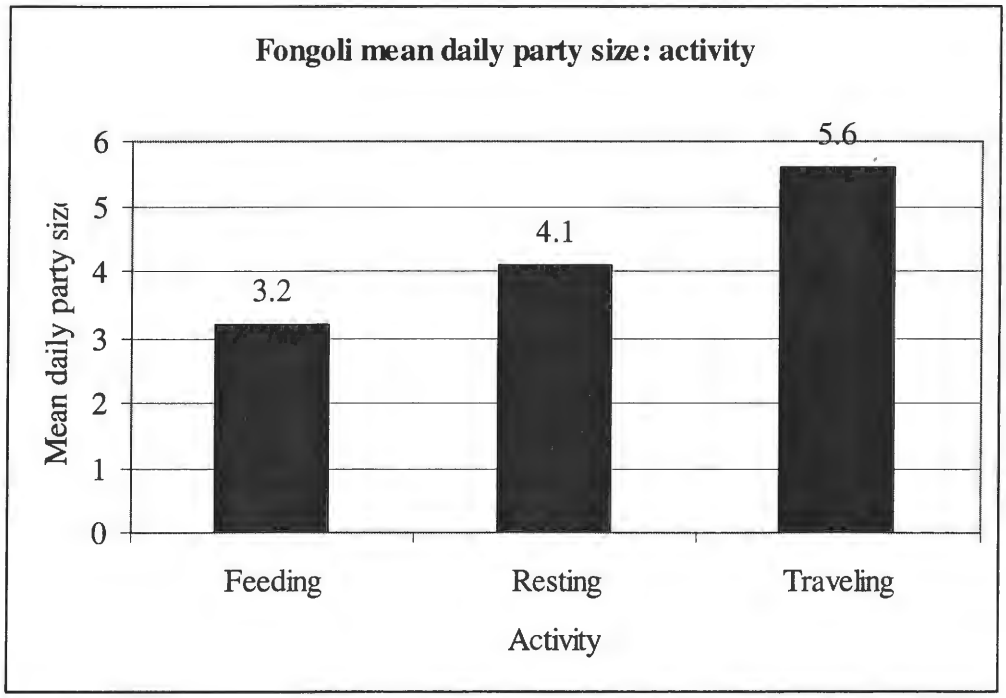


Fig. 5.11. Compares average mean party size and activity. Mean party size for observed traveling parties (7.92) was over twice that of feeding parties.

Fig. 5.12. A Fongoli adult female seen resting above a water hole (Photo courtesy of F. Stewart)

data available on estrous female effect on a savanna community, parties were observed 63 times with anogenitally swollen females, with party size mean found to be 7 (compared to

4.6 normally) (Tutin et al., 1983). In the current study, at least one estrous female was seen in parties 16 times total (two estrous females were observed on six occasions), with mean party size of these groups being considerably larger than others (mean = 8.1, SD = 3.8, Figure 5.13.). Although only a third of these observations were considered complete counts, the numbers reflect all observed individuals and so *underestimate* total party size. Very large parties with estrous females were seen throughout the study period, although how savanna chimpanzees balance large parties with hypothesized scare resources (e.g. during the dry season) remains unanswered (see below).

Habitat

Table 5.4. presents the mean party sizes observed in different habitats. The data presented here are from complete chimpanzee party counts only (N=27) and do not include infants. Average party size was larger (5.3.) in woodland areas than in moist ones (3.5) by over 50 results seen at Mt. Assirik (Tutin et al., 1983, Table 7). Figure 5.14. uses all chimpanzee encounters and attempts to compare the proportion of time researchers spent in

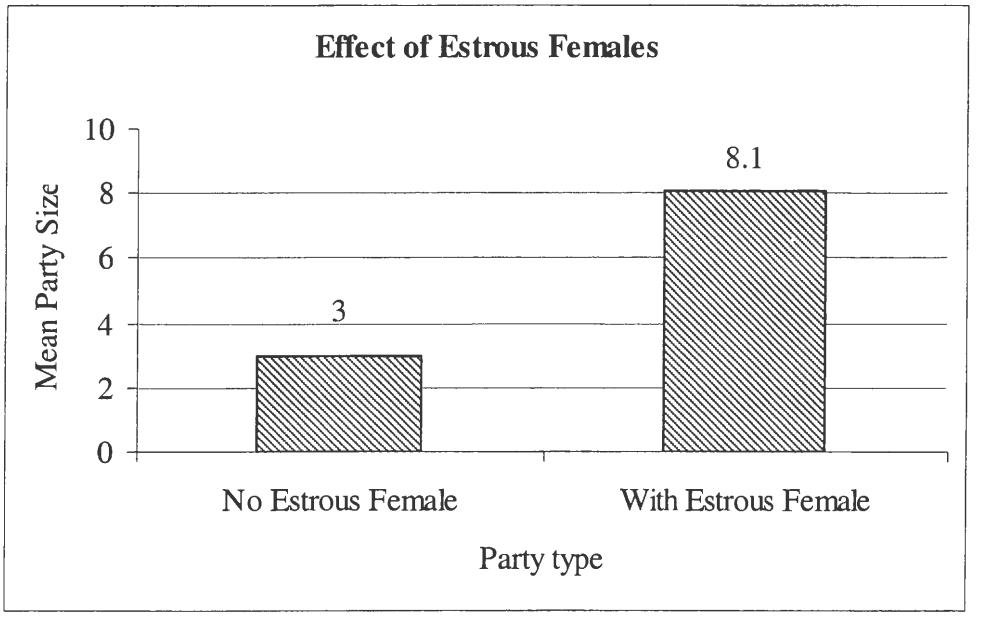


Fig. 5.13. The effect of estrous female presence (N=15) on mean party size in the Fongoli community

each habitat[6] with the percentage of encounters, testing the aforementioned "habitat-preference" %, though more chimpanzee encounters were made in moist habitats, paralleling the suggestion by Tutin et al. (1983). Parties were seen 64% of the time in moist habitats, despite researchers only dedicating 23% of their surveying time there. Whereas in other savanna habitats chimpanzees are predicted to spend more time in woodlands that may provide food sources and refuges from potential predators (Moore, 1992), this is unlikely to be seen at Fongoli. Not only have most terrestrial predators been extirpated, but the woodlands in this region do not mimic those of other savanna sites (Hernandez and Moore, pers. comm.). Woodland canopies are not connected at Fongoli and with permanent water sources widely distributed (see Chapter Four), shaded and wetter areas are likely to be highly valued, especially in the dry season months.

TABLE 5.4. summarizes complete party counts made in various habitat types. In only moist and woodland habitats were complete party counts made

Habitat Type	Complete Parties	Mean Party Size
"Moist"	19	3.5
Woodland	8	5.3
Grassland	NA	NA
Plateau	NA	NA

Summary

Mean daily party size for Fongoli chimpanzees was found to be 4.1 individuals, with most encountered parties (18%) being individual chimpanzees. Whether dependent offspring are included in the definition of 'party' does have a significant effect on reported results and the same is expected when other definitions are applied (see Chapter 1, Table 1.1). Frequency distributions from other savanna (Mt. Assirik) and forest (Bossou) sites from West Africa suggest common trends in researcher-chimpanzee encounters, although at Fongoli no reliably significant relationships were found between party size and either habitat

[6] Despite the current study recognizing three different wet habitats (namely gallery forest, ecotone, and marigot - see Chapter Four for descriptions of each), results here will group these three types into one: "moist" (see Figure 5.11. due to their each being sources of water early into the dry season).

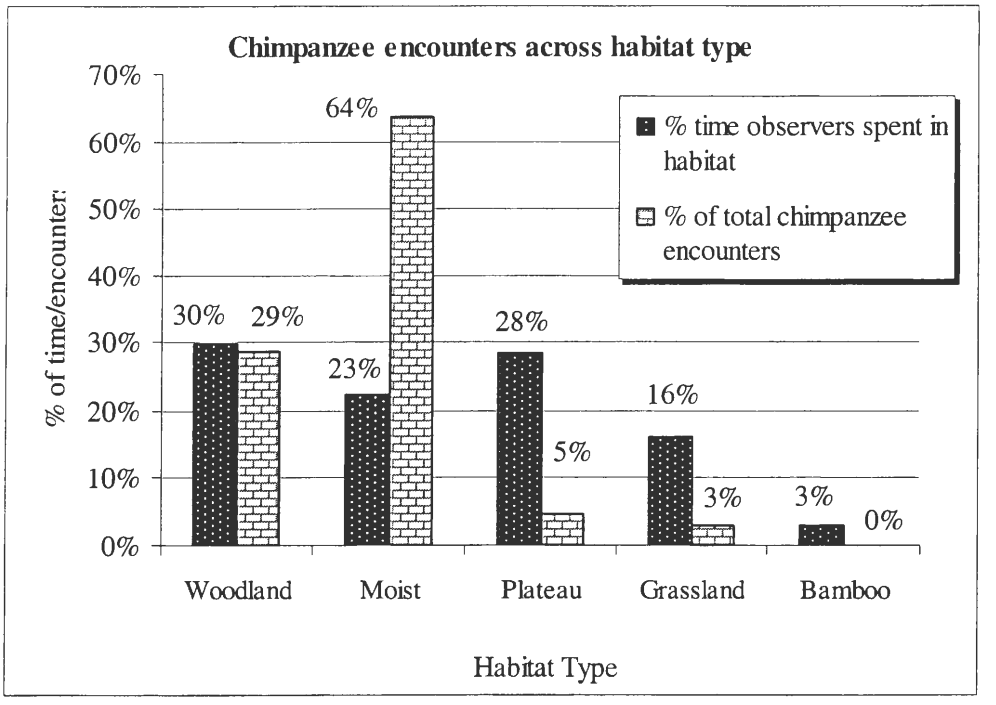


Fig. 5.14.Frequency of total chimpanzee encounters for each habitat type

or activity. However, similar to most known sites, all large parties contained at least one estrous female and like results from Mt. Assirik from the 1970s, traveling parties at Fongoli were consistently the largest. If this is not due to chimpanzee-avoidance, it is thought to be a savanna adaptation: to maintain contact while moving throughout a larger home range (Hunt and McGrew, 2002; Moore, 1992). Larger parties were found when chimpanzee vocalizations were used as the means of locating parties (vocalizations, mean = 5.24, N=40; sighting, mean = 2.06, N=15; T-test, P=.0107), mimicking patterns seen in at least two other communities in East Africa. Finally, Fongoli chimpanzees spend most of their time in wet, closed habitats where shade and water are thought to be more available.

5.5 Discussion

Party size at Fongoli (4.1, N=27) did not differ from that found at Mt. Assirik from the early 1970s in the only other behavioral study of Sénégalese chimpanzees. There, mean party size was observed to be 4.6 individuals (N=168, Baldwin, 1979). Despite similar findings at other well known sites (4.2 - Gombe National Park Tanzania - Teleki, 1977; 4.4 – Budongo Forest, Uganda – Sugiyama, 1968), party size has historically showed tremendous range across different study sites (see Table 5.2.) from 3.9 (Reynolds and Reynolds, 1965) to 10.27 (Mitani et al., 2002).

Definition matters

Attempts to standardize data collection methods for observed behaviors have not yet included 'party.' Instead, researchers continue to use various definitions in their criteria of chimpanzee social grouping (see Chapter One, Table 1.1.). Unable to systematically test these different definitions with a not-yet fully habituated community, only rarely could I apply multiple definitions to the same party. During these few instances, however, it was clear that party size count would vary as definition does, especially when definitions include ecological features that vary between savanna and forested habitats. For example:

1. **Inter-individual distance** (e.g. 30 meters – Sakura, 1994; 100 meters – Wrangham and Smuts, 1980, etc.): The distance between chimpanzees within a party is suspected to depend on numerous variables, namely resource distribution, home range, etc. With all of these likely to be greater in savanna areas, using them as part of criteria will warrant site-specific definitions.
2. **Auditory/Visual contact** (Sugiyama and Koman, 1979; Boesch, 1991, 1996) – If chimpanzee parties show "amoeba like" movements (Pepper et al., 1999) or "coordinated behavior" (Newton-Fisher, 1999), then using auditory and/or visual contact can be problematic. Individuals, especially in savanna sites where visibility can reach 200 meters (pers. obs.) and vocalizations are thought to carry as far as five kilometers (pers. obs.), could theoretically maintain both auditory and/or visual

contact and yet not show coordinated movements or behavior. Thus these criteria seem unhelpful.

There appear, then, to be two options from which researchers must choose when studying grouping behavior in chimpanzees. The first is to continue creating a new definition of 'party' for each study, at each location, thus making cross-community comparisons extremely challenging. The advantage to this strategy is that it provides researchers with pertinent information regarding the temporal and spatial dynamics interacting in a particular community. The alternative, however, is to follow Newton-Fisher's (1999) suggestion of using, not independent features of the habitat or arbitrary distances between individuals, but the *actual* behavior of the chimpanzees themselves. While estimating the mean distance between individuals in a party (35 meters), he emphasized the most reliable characteristic of chimpanzee parties: that individuals show coordinated behavior (Newton-Fisher, 1999).

Detection Method

Previous studies have demonstrated that larger parties with more individuals call more frequently and louder than smaller ones with fewer individuals (Goodall, 1986; although see Mitani and Nishida, 1993). This pattern was reflected in the mean party sizes observed for each method and mirrors trends seen in other communities (Figure 5.10.). It was initially thought that the significant difference between these means was an artifact of the combined openness of the habitat with studying a partially-habituated community (i.e. individuals that are not comfortable with researchers will perceive them sooner and have adequate time to avoid them). However, Figure 5.9. clearly suggests that this trend is independent of study-site and habitat-type (Kanyawara and Ngogo communities are found in Kibale National Park, Uganda, a combined tropical lowland and deciduous forest).

Activity

Feeding

The results of the current study suggest that Fongoli chimpanzees are feeding in smaller parties (3.2) than at other sites (Boesch-Boesch-Achermann, 2000; although see

Goodall, 1986). This number may be lower for one of two reasons. It may be an underestimate considering the current habituation level of the Fongoli community. Premature fleeing by individuals will reduce the number of observed chimpanzees engaged in other activities. Second, Fongoli chimpanzees may actually form smaller feeding parties because of real differences in food availability and patch quality. Nonetheless, at most other sites, feeding parties have been observed to be larger (Table 5.5.) than during other activities. Whether this is an artifact of larger total community sizes or actual grouping behavior is not yet known. Hunt and McGrew (2002) suggested that savanna communities may aggregate in larger parties to maintain contact when feeding and traveling in these arid habitats. However,

TABLE 5.5. Comparison of feeding parties at various other savanna and forested sites

Community name, Country	Feeding Party Size	Estimated Community Size	Reference
Semliki Wildlife Reserve, Uganda*	4.8	NA	Hunt and McGrew, 2002
Mt. Assirik, Sénégal*	6.0	24	Tutin et al., 1983
Tai Forest, Ivory Coast	9.9-10.1	76	Boesch and Boesch-Achermann, 2000
Bossou, Guinea	3.6 – 5.7	20	Sakura,1994
Fongoli, Sénégal*	3.2	27	Current study

* denotes savanna communities

a more likely scenario is that these chimpanzees form smaller daily parties to search out sufficient food and water sources, but re-aggregate at night in larger parties to maintain social cohesion (see Discussion, Chapter Six; Hernandez, pers. comm.). The data from Fongoli support this latter hypothesis.

Traveling and other likely influences

Traveling parties observed at Fongoli (5.6) were found to be significantly larger those engaged in other activities (Figure 5.11.). This phenomenon was seen at Mt. Assirik also, where traveling parties had a median size of 19 individuals (Tutin et al., 1983), compared to 3.5 at Fongoli. Moreover, at Fongoli all observed parties of greater than six individuals

contained at least one estrous female, indicating that these larger parties were probably formed in response to increased mating opportunities. It is possible, though, that the large parties seen in these savanna communities are a strategy invoked to maintain contact, as Moore (1992) and Hunt and McGrew (2002) have suggested. These data contrast sharply with what is found at other, forested sites where the largest parties are reliably formed, if not because of estrous females, for congregations at high quality food patches or hunting. Goodall (1968) observed largest parties to aggregate during feeding bouts whereas at Tai (Boesch and Boesch-Achermann, 2000; Andersen et al., 2002) and Kibale (Wrangham et al., 1992; Chapman et al., 1995; Mitani and Watts, 1999; Mitani et al., 2002) National Parks, meat eating draws larger than normal feeding parties.

Chimpanzees at Fongoli are not predicted to feed in such large aggregations because of the widely distributed food sources (see Chapter Four). Instead, data suggest that they disperse into smaller parties to exploit numerous small patches (see similar behavior at Budongo, Newton-Fisher et al., 2000). If true, this behavior would conform to one of the predictions made for savanna chimpanzees and how they adapt to living in such an open habitat. Moore (1992) suggested that to compensate for such a large home range, savanna chimpanzees may monitor each other more vocally throughout the day, or use predictable travel routes between resources and nesting sites. An alternative means of coping with living in such an area is to travel between core areas in large parties and then disperse once a party has arrived at a particular destination, perhaps, "with lower frequencies of reunions between community members" (Moore, 1992:109). Savanna chimpanzees may shift core areas by traveling in large parties, then settle for extended periods in particular areas with seasonally available fruiting trees. During daily excursion parties, then, are hypothesized to be small, with larger aggregations forming at night (see Discussion, Chapter Six).

Other influences

Estrus

Figure 5.13. shows clearly that Fongoli chimpanzee mean party size was larger when estrous females were present. A future study, however, might address if, and to what extent, female reproductive behavior responds to such extreme ecological conditions. Aggregating in

Fig. 5.15. An adult male chimpanzee retreats after spotting researchers

such large parties when food and water resources are scarce and patchily distributed may be difficult to exploit communally. Do estrous cycles of savanna chimpanzee females respond to the extreme nature of their habitat such as to reduce the chances of causing these large parties to form when ecological conditions cannot support them? Future studies may want to address this.

Habitat

Savanna and forest-dwelling chimpanzees show differential patterns in social grouping (Figure 5.9.). The habitat types of the Fongoli community are detailed in Chapter Four and are thought to mimic those described by Tutin et al. (1983) in their study of chimpanzees in the PNNK. The authors of that study concluded that the habitat types were not equally represented in the study area and that chimpanzees there appeared select to specific ones, especially during the very hot and dry season. For example, with water sources drying and temperatures soaring in the mid-late dry season (March-May), the Assirik chimpanzees were found to spend more time in gallery forests than other habitats, likely drawn there for the cooler temperatures and increased moisture present (Tutin et al., 1983; Hunt and McGrew, 2002). Recent studies examining chimpanzee terrestriality have likewise supported this idea, suggesting that these apes' movement and location is a function of temperature and available resources (Takemoto, 2004). If Fongoli chimpanzees conform to the same patterns observed at Assirik and Bossou, then they should spend more time in

gallery and marigot woodland habitats, avoiding the more open areas like plateaus and grassland where they are more exposed to both heat and (when present) predators.

At Fongoli, between May and December 2003, parties were most often seen in wetter, closed areas (Figure 5.14.; see also Chapter Four for description), probably to exploit the shade and cooler temperatures these areas provide. Infrequency of chimpanzee encounters on plateau and grasslands at Fongoli is probably not, as suggested by Hunt and McGrew (2002), an artifact of predator avoidance mechanisms (most large predators have been exterminated at Fongoli), but rather the result of parties moving quietly along the periphery, usually through ecotone habitats, sheltered from the radiating heat off the laterite (pers. obs.). Whereas Fongoli chimpanzees are thought to avoid these open areas year round, it is suspected that increasingly more time is spent in moist, covered areas during the dry season (December-May - Pruetz unpublished data), observed also at Mt. Assirik and Semliki.

Food and water distribution

Adopting behavior to scarce resources is not atypical for primates. Scholz and Kappeler (2004) found that red-fronted lemurs *(Eulemur fulvus rufus)* employee various drinking and ranging strategies as a product of how far their core range is from permanent water sources. Similar results were found in a group of capuchin monkeys *(Cebus apella nigritus)* living in Iguazu National Park, Argentina. Di Bitetti (2001) suggested that these monkeys expand day range and sleeping sites as resources, particularly water, become less available in the winter months. Chimpanzees are no different, with feeding strategies varying as do available resources. For example, chimpanzees are known to disperse into small groups to cover greater distances in search of ripe fruits when such are unavailable [versus, for example, gorillas *(Gorilla gorilla)* who will modify their diet instead] (Tutin and Fernandez, 1985). In fact, chimpanzee range has been seen to grow from 5 km^2 in rich habitats to more than 400 km^2 in poorer ones (Reynolds, 1981).

Figure 5.16. clearly suggests that with the arrival of the first rains (June/July), mean *daily* party size began to grow steadily, not decreasing until the very end of the wet season in late October. These data may suggest that Fongoli chimpanzees increase mean party size as water becomes more readily available and decrease party size as water becomes less

available as groups travel farther to find adequate sources (Chapman and Chapman, 2000). But what about their response to widely distributed food sources, not just water ones?

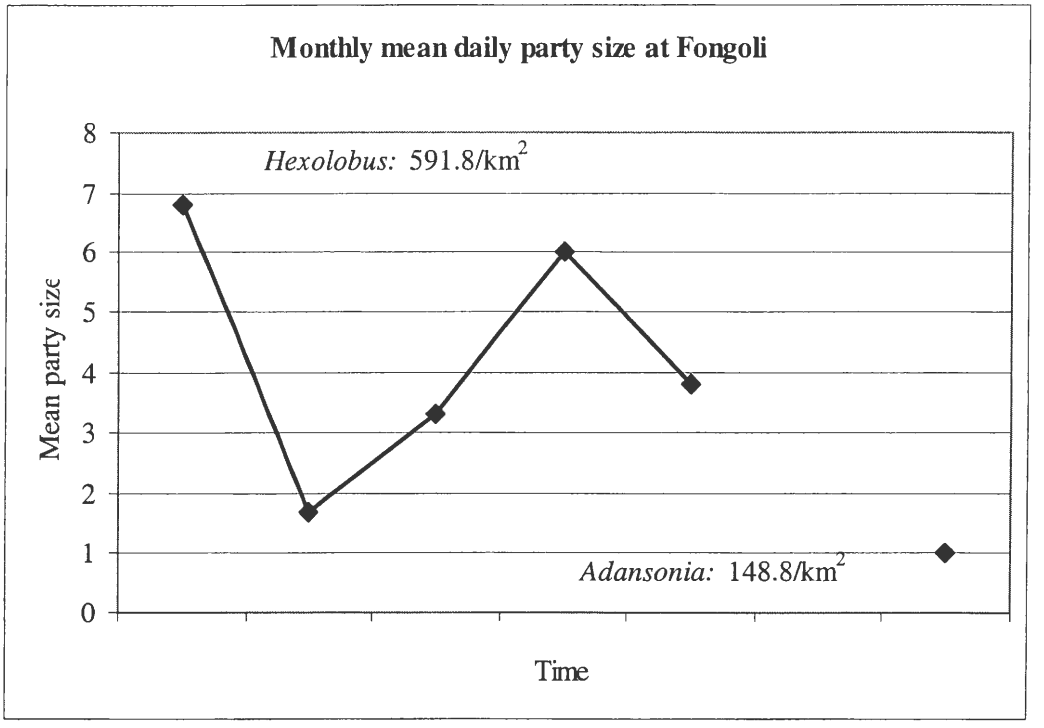


Fig. 5.16. Mean daily party size over the study period, from early wet season (June) to early dry season (December). The trend here supports predictions that chimpanzee mean party size decreases as the dry season arrives and some resources (e.g. water) become less readily available.

It was hypothesized that chimpanzees should reduce party size in response to more widely distributed food sources (see Chapter One, Hypothesis # 1). To support this, during times when, for example, *Adansonia,* is observed to be the dominant food source for the Fongoli chimpanzees (November-January, Pruetz, unpublished data), party size should be smaller than seen at other times of year. Although no data were available during November for daily party size, it is lowest during the month of December and is thought likewise to be low during November as well (see trend in Figure 5.16.; pers. obs.). Similarly, it was thought that when *Hexolobus,* a commonly found fruit throughout the study area, is consumed most (September and October, Pruetz, unpublished data), mean monthly chimpanzee party size should be highest. Again, data collected on monthly mean party size at Fongoli support this.

It can be preliminarily concluded that Fongoli chimpanzees seasonally adjust party size in response to feeding tree distribution. If this is the case, such behavioral adaptations to ecological conditions would parallel similar patterns seen at other sites where chimpanzee

party size fluctuates as does, for example, fruit availability (Goodall, 1986; Sakura, 1994; Doran, 1997; Matsumoda-Oda, 1999; Boesch and Boesch-Achermann, 2000; Hashimoto et al., 2001, 2003; Matsumoda-Oda et al., 2001). Here, though, it is reported that mean chimpanzee party size shows an inverse relationship with the distance between feeding trees, not fruit abundance as studied elsewhere. This trend conflicts with what has been observed in other savanna communities, where chimpanzees "assumed a state of congregation and started a rapid movement" when "food supply was scanty" (Izawa, 1970:24). Nonetheless, it is therefore suggested that reducing party size may be a response to increased travel costs incurred by having to move between widely distributed food sources (Janson and Goldsmith, 1995; Chapman and Chapman, 2000).

Considering the nature of this open habitat (McGrew et al., 1981; Moore, 1992), how are savanna chimpanzees able to maintain communication and social cohesion if individuals of a single community are forced to divide into smaller parties and travel far to access necessary resources? Data from Mt. Assirik indicated traveling parties were significantly larger than parties seen in any other activity (Tutin et al., 1983). The same was seen at Fongoli (Figure 5.11.), despite general trends towards the formation of smaller parties. It was also proposed that chimpanzees should thus follow 'predictable routes' to sustain contact with each other: these were likewise found frequently at Fongoli throughout the study period (pers. obs.). A final possibility is that savanna chimpanzees aggregate in larger nest groups at night after increased dispersion during the day. A mean nesting party size greater than mean day party size would suggest such a phenomenon (see Chapter Six).

Summary

Kédougou is growing rapidly with the population thought to have doubled since 1970 (Sall, 2000). The expansion of surrounding villages and overall growth of the town population continue to threaten resources shared by people and chimpanzees (Knutsen, 2003). As Kédougou and, consequently, the needs of its inhabitants increase, more land is converted for agriculture and more exploitation of natural resources is observed (Knutsen, 2003). The current study examined how scarce and widely distributed resources, under threat and competition from humans, influence chimpanzee grouping patterns. When data on

Fig. 5.17. A baobob *(Adansonia digitata)* tree in the study area.

monthly mean party sizes was examined during the times of year these species (here, *Adansonia* and *Hexolobus)* dominate the diet of Fongoli chimpanzees, mean daily party size was found to be higher as the density of that particular species increased. Likewise, as a particular feeding tree species was found to be less abundant (e.g. *Adansonia)* party size decreased. These relationships suggest that Fongoli chimpanzee daily party size may change as a response to feeding tree distribution/patch size. It is well accepted (Goodall, 1986; Sakura, 1994; Doran, 1997; Matsumoda-Oda, 1999; Boesch and Boesch-Achermann, 2000; Hashimoto et al., 2001, 2003; Matsumoda-Oda et al., 2001) that chimpanzees modify their social grouping patterns in response to fruit availability; Data reported here from the Fongoli community, however, suggest that savanna chimpanzees may likewise respond to the distribution of fruit sources as well as its abundance.[7]

Previous studies of chimpanzee social grouping consistently reveal temporal variation in party size. And although food availability and estrous female presence have been long thought to be key determinants of party size and composition in chimpanzees, no study has yet been able to confirm this in savanna communities (although see Tutin et al., 1983). The

[7] To my knowledge, no study has yet examined the relationship between savanna chimpanzee party size and fruit abundance

current study found that chimpanzee daily parties reflect the distribution of their food sources at certain times of year. If this is the case, then this community would conform, in part, to Moore's (1992) predictions for savanna chimpanzee adaptations.

Sources

Anderson DP, Nordheim EP, Boesch C, Moermond TC. 2002. Factors influencing fission-fusion grouping in chimpanzees in the Tai National Park, Cote d'Ivoire. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 90-101.

Balcomb SR, Chapman CA, Wrangham RW. 2000. Relationship between chimpanzee *(Pan troglodytes)* density and large, fleshy-fruit tree density: Conservation implications. *Amer J of Primatol* 51:197-203.

Baldwin PJ. 1979. The natural history of the chimpanzee *(Pan troglodytes verus)* at Mt. Assirik, Senegal. Unpublished Ph.D. thesis, Stirling: University of Stirling.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *International J of Primatol* 3(4):367-385

Boesch C. 1991. The effects of leopard predation on grouping patterns in forest chimpanzees. *Behaviour* 117:220-242.

Boesch C. 1996. Social grouping in Tai chimpanzees. In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 101-113.

Boesch C. 2002. Cooperative hunting roles among Tai chimpanzees. *Human Nature-Int Bios* 13(1):27-46.

Boesch CA, Boesch-Achermann H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Amer J of Phys Anthropol* 78:547-573

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Bouliere F, Hadley M. 1970. The ecology of tropical savannas. *Ann Review of Ecology and Systematics* 1:125-152.

Chapman CA. 1986. *Boa Constrictor* predation and group response in white-faced cebus monkeys. *Biotropica* 18(2):171-172.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: The importance of travel costs. In: Boinski S, Garber PA, editors, *On the move: How and why animals travel in groups,* Chicago and London: University of Chicago Press. p 24-42.

Chapman CA, White FJ, Wrangham RW. 1993. Defining subgroup size in fission-fusion societies. *Folia Primatol* 61:31-34.

Chapman CA, White FJ, Wrangham RW. 1994. Party size in chimpanzees and bonobos: A reevaluation of theory based on two similarly forested sites. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors, *Chimpanzee Cultures*, Cambridge: Harvard University Press. p 41-58.

Chapman CA, Wrangham RW, Chapman CA. 1995. Ecological constraints on group size: an analysis of spider monkey and chimpanzee subgroups. *Behav Ecol Sociobiology* 36:59-70.

Clavette K. 2003.Conservation through Folklore: Ethnoprimatology in Southeastern Sénégal. Unpublished MA Thesis: Northern Arizona University.

Di Betti MS. 2001. Home-range use by the tufted capuchin monkey *(Cebus apella nigritus)* in a subtropical rainforest of Argentina. *J of Zoology* 253:33-45.

Doran D. 1997. Influence of Seasonality on activity patterns, feeding behavior, ranging and grouping patterns in Tai chimpanzees. *Int'l J of Primatol* 18(2):183-206.

Duvall CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21(4):173-203.

Ghiglieri MP. 1984. *The chimpanzees of the Kibale Forest.* New York: Columbia University Press.

Goodall J. 1965. Chimpanzees of the Gombe Stream Reserve. In: Devore I, editor, *Primate Behavior*, New York: Holt, Rinehalt, and Winston. p 425-473.

Goodall J. 1968. Behaviour of free-ranging chimpanzees of the Gombe Stream Area. *Animal Behaviour Monograph* 1:163-311.

Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: The Belknap Press of Harvard University.

Hashimoto C, Furuichi T, Tahiro, Y. 2001. What factors affect the size of chimpanzee parties in the Kalinzu Forest, Uganda? Examination of fruit abundance and number of estrous females. *Int'l J of Primatol* 22(6):947-949.

Hashimoto C, Suzuki S, Takenoshita Y, Yamagiwa J, Basabose AK, Furichi T. 2003. How fruit abundance affects the chimpanzee party size: a comparison between four study sites. *Primates* 44:77-81.

Hrdy SB. 1999. *Mother Nature: A History of Mothers, Infants, and Natural Selection.* New York City: Pantheon.

Hunt KD, McGrew WC. 2002. Chimpanzees in the dry habitats of Mont Assirik, Sénégal and Semliki Wildlife Reserve, Uganda. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 35-51.

Isbell LA. 1991. Contest and scramble competition: patterns of female aggression and ranging behavior in primates. *Behav Ecol* 2:143-155.

Itani J, Suzuki A. 1967. The social unit of chimpanzees. *Primates* 8:355-381.

Izawa I. 1970. Unit groups of chimpanzees and their nomadism in the savanna woodland. *Primates* 11(1): 1-46.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326-336.

Knutsen PG. 2003. Threatened existence: *Saba senegalensis* in southeastern Senegal. Unpublished MA thesis, Ames: Iowa State University.

Lawesson LE. 1995. *Studies of woody flora and vegetation in Senegal.* Copenhagen: Council for Nordic Publications in Botany.

Matsumoto-Oda A. 1999. Mahale Chimpanzees: Grouping patterns and cycling females. *Amer J of Primatol* 47:197-207.

Matsumoto-Oda A, Osaka K, Huffman MA, Kawanaka K. 1998. Factors affecting party size in chimpanzees of the Mahale Mountains. *Int'l J of Primatol* 19(6):999-1011.

McDaniel PS. 1995. The social behavior and ecology of the black-handed spider monkey *(Ateles geoffroyi)*. Unpublished Ph.D. thesis, St. Louis: Saint Louis University.

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirk, Sénégal, West Africa. *J of Human Evolution* 10:227-244.

McGrew WC, Baldwin PJ, Tutin CEG. 1988. Diet of wild chimpanzees *Pan troglodytes verus)* at Mt. Assirik, Senegal: I. Composition. *Am, J. of Primatol* 16:213-226.

Mitani JC, Nishida T. 1993. Contexts and social correlates of long distance calling by male chimpanzees. *Animal Behavior* 45:735-746.

Mitani JC, Watts DP. 1999 Demographic influences on the hunting behavior of chimpanzees. *American J of Phys Anthropol* 109(4):439-454.

Mitani JC, Watts DP, Lwanga JS. 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 102-111.

Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol* 11(1):9-25.

Moore J. 1992. 'Savanna chimpanzees'. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics on Primatology, Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 99-118.

Morgan D, Sanz C. 2003. Naive encounters with chimpanzees in the Goualougo Triangle, Republic of Congo. *International J of Primatol* 24(2):369-381.

Newton-Fisher NE 1999. Association by male chimpanzees: A social tactic. *Behaviour* 136:705-730.

Newton-Fisher NE, Reynolds V, Plumptre AJ. 2000. Food supply and chimpanzee *(Pan troglodytes schweinfurthii)* party size in the Budongo Forest Reserve, Uganda. *International J of Primatol* 21(4):613-628.

Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.

Nishida T. 1979. The social structure of chimpanzees at the Mahale Mountains. In: Hamburg DA, McCown, ER, editors, *The Great Apes,* Menlo Park: Benjamin Cummings. p 73-121.

Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International J of Primatol* 20(5):613-632.

Pruetz JD. 2002. Competition between savanna chimpanzees and humans in southeastern Sénégal. *Amer J Phys Anthropol* 128-128 Suppl. 34 2002.

Pruetz JD, Knutsen P. 2003. Scrambling for a common resource: Chimpanzees, humans, and *Saba senegalensis*, in southeastern Sénégal. *Amer J Phys Anthropol* 172-172 Suppl. 36

Pruetz JD, Leasor HC. 2002. Survey of three primate species in forest fragments at La Suerte Biological Field Station, Costa Rica. *Neotropical Primates* 10(1):4-8.

Pruetz JD, Marchant LF, Arnot J, McGrew WC. 2002. Survey of chimpanzees *(Pan troglodytes verus)* in southeastern Sénégal. *American J of Primatol* 58:35-43.

Reynolds PC. 1981. *On the Evolution of Human Behavior.* Berkeley: University of California Press.

Reynolds V, Reynolds F. 1965. Chimpanzees in the Budongo Forest. In: Devore I, editor, *Primate Behaviour,* New York: Holt, Rinehard and Winston. p 368-424.

Ross C. 2001. Park or ride? Evolution of infant carrying in primates. *Int'l J of Primatol* 22(5):749-771.

Sabater-Pi J. 1979. Feeding behaviour and diet of chimpanzees *(Pan troglodytes troglodytes)* in the Okoroobiko Mountains of Rio Muni (Republic of Equatorial Guinea), West Africa. *Primates* 15:351-364.

Sakura O. 1994. Factors affecting party size and composition of Chimpanzees *(Pan troglodytes verus)* at Bossou, Guinea. *Int'll J of Primatology* 15(2):167-183.

Sall M. 2000. *Atlas du Senegal.* Paris: Les Editions J.A.

van Schaik CP. 1983. Why are diurnal primates living in groups? *Behaviour* 41: 87:120-144.

van Schaik CP. 1989. The ecology of social relationships among female primates. In: Standen V, Foley RA, editors, *Comparative Socioecology,* Cambridge: Cambridge University Press. p 195-218.

Scholz F, Kappeler PM. 2004. Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus. Int'l J of Primatol* 25(3): 599-613.

Sterk EHM, Watts DP, van Schaik CP. 1997. The evolution of female social relationships in nonhuman primates. *Behav Ecol Sociobiol* 41:291-309.

Sugiyama Y. 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1976-1980. *Primates* 22(4):435-444.

Sugiyama Y. 1999. Socioecological factors of male chimpanzee migration at Bossou, Guinea. *Primates* 40(1):61-68.

Sugiyama Y, Koman, J. 1979. Social structure and dynamics of wild chimpanzees at Bossou, Guinea. *Primates* 20(3):323-339.

Suzuki A. 1969. An ecological study of chimpanzees in a savanna woodland. *Primates* 10:103-148.

Symington MM. 1987. Ecological and social correlates of party size in the black spider monkey, *Ateles paniscus chamek.* Unpublished Ph.D. thesis, Princeton, New Jersey: Princeton University.

Takemoto H. 2004. Seasonal change in terrestriality of chimpanzees in relation to microclimate in the tropical forest. *Am J of Phys Anthropol* 124(1):81-92.

Teleki G. 1973. *Predatory Behaviour of Wild Chimpanzees.* Lewisburg, Pa: Bucknell University Press.

Treves A, Chapman CA. 1996. Conspecific threat, predation avoidance, and resource defense: Implications for grouping in langurs. *Behav Ecol Sociobiol* 39(1):43-53.

Tutin CEG, Fernandez M. 1985. Foods consumed by sympatric populations of *Gorilla gorilla gorilla* and *Pan troglodytes troglodytes* in Gabon: some preliminary data. *Int'l J of Primatol* 6:27-43.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

White FJ, Wrangham RW. 1988. Feeding competition and patch size in the chimpanzee species *Pan paniscus* and *Pan troglodytes. Behaviour* 105:148-164.

Wrangham RW. 1977. Feeding behavior in chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor, *Primate Ecology*, London: Academic Press. p 504-538.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. *Behaviour* 75:262-300.

Wrangham RW. 2000. Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In: Kappeler P, editor, *Primate Males*, Cambridge: Cambridge University Press. p 245-258.

Wrangham RW, Clark AP, Isabirye-Basuta G. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics in Primatology Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 81-98.

Wrangham RW, Conkilin-Brittain NL, Hunt KD. 1998. Dietary response of chimpanzees and cercopithecines to seasonal variation in fruit abundance. I. Antifeedants. *Int'l J of Primatol* 19(6):949-970.

Wrangham RW, Gittleman JL, Chapman CA. 1993. Constraints on group size in primates and carnivores: Population density and day-range assays of exploitation competition. *Behav Ecol Sociobiol* 32:199-209.

Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe Stream National Park, Tanzania. *J Reprod Fert* 28:13-31.

Chapter Six: Nesting party size

6.1 Introduction

All wild great apes beyond infancy construct nightly (and sometimes, although less often, daily) nests. None of these nests, however, serve as a home-base (Hediger, 1977) as in many other species (see below). The availability of data on chimpanzee nesting behavior does not mimic, at least in abundance, that of social behavior. Despite early efforts to understand even the most fundamental aspects of this ape behavior (Goodall, 1962; Bernstein, 1967; Martin, 1975; Hediger, 1977), studies rarely focus on the phenomenon (although see Baldwin et al., 1981; Fruth & Hohmann, 1994, 1996; Fruth, 1995), instead using it as a means to some greater ends (Sept, 1998; this study) or addressing it as it relates to other aspects of ape socio-ecological behavior (Baldwin et al., 1981). Until recently, the majority of studies used nest counts merely as a means of censusing unknown chimpanzee populations (Tutin & Fernandez, 1984; Plumtre & Reynolds, 1997; Blom et al., 2001; Pruetz et al., 2002), rather than indicators of ecological dynamics (although see Fururchi et al., 2001a, b; Furuchi and Hashimoto, 2004).

Goodall (1962) was one of the first researchers to systematically examine and record data on various aspects of wild chimpanzee nesting behavior. Reporting on the influences of nesting site, she suggested that food availability was the ultimate determinant in where chimpanzees decided to nest and that only when ripe fruits were seasonally abundant would many chimpanzees nest in a single tree. This was contrary to earlier claims that suggested ape nesting behavior (the only of its kind within the Order Primates) evolved in response to predation pressure (Nissen 1931). Nests were thereafter used primarily as evidence of chimpanzee existence, not as indicators of their cognitive abilities, social structure, or ecological resource availability. Furthermore, almost all studies examining nesting behavior have been conducted in tropical forests where numerous chimpanzee communities are now habituated, with few focusing on this behavior in savanna chimpanzee populations. One early study compared those nests made by chimpanzees at Mt. Assirik, Sénégal, within the Parc National du Niokola Koba (PNNK), with those of a community in

Equatorial Guinea. Baldwin et al. (1981) found that nesting behavior differed between the two communities in every aspect measured[1], save for nearest nest distance; variation in all cases, however, could have been attributed to ecological differences between the study sites such as predation pressures, seasonal differences, and vegetation densities. Mean nest party size at Mt. Assirik was found to be 5.2 nests/group (calculated from Baldwin et al., 1981, Figure 2), with chimpanzees nesting most often in gallery forest patches thought to provide more available trees (Baldwin, 1979).

In the only other known study involving savanna chimpanzee nesting behavior, Sept (1998) used nesting behavior in chimpanzees to explore how human land use has affected ranging behavior and nesting patterns in a population of chimpanzees in central Africa. Although unable to conclude whether or not current chimpanzee nesting behavior is representative of the "ancestral suite of behaviors recognized in living hominoids" (p.88), Sept was the first to attempt to use chimpanzee nesting behavior as a means of assessing early hominin evolution. Her study of nests in the dry region of Ishasa, eastern Zaire, provided evidence of "spatially redundant" (Sept, 1992:194) behavior in the chimpanzee nest groups there, suggesting their repeated use of particular, preferred nesting areas. Without available data, however, on chimpanzee community size or local tree densities, the study was unable to draw strong conclusions either on nesting behavior or how it may accurately represent early hominin home bases.

Despite these early efforts to use and understand chimpanzee nesting behavior, implications of nest construction are fourfold. First, its appearance in both the prosimians (Charles-Dominque, 1977) and the great apes, but not in Old or New World monkeys, suggests the behavior has evolved twice in the Order Primates (Hediger, 1977; Fruth, 1995). In spite of structural similarity observed between most animal nests, the functional explanation for them, even within the Order, shows great variation (Groves and Sabater Pi, 1985). In prosimians, for example, infants are often "parked" in nests when they are young and unable to grasp onto traveling and foraging mothers (Fietz, 1999). These spots also frequently serve as locations for prolonged hibernation periods observed in some Malagasy

[1] These included mean height of nests, number of nests/group, number of nests/tree, and minimum distance between nests (Baldwin et al., 1981, Table 1)

species (Fietz, 1999; Wright, 1999) and so may be more analogous to those assembled by some small mammals (e.g. rabbits, shrews – Martin, 1975) than to the apes. Hediger (1977) attempted to differentiate the nests made within the Order Primates. For prosimians and 'lower' primates, he suggested that the functions of nests are twofold: the first was to represent a temporary fix-point of breeding and for rearing offspring. The second, what he called "the home," was more solid, secure, durable, and permanent, possibly being passed down over generations. Ape nests, on the other hand, are created purely for sleep and have "nothing in common with true breeding nests" (Hediger, 1977:185). Chimpanzees, along with gorillas and orangutans, on the other hand, have never been observed to spend consecutive nights in the same nest (although some nests may be re-built at a later time). Moreover, chimpanzees neither park their infants in these nests nor hibernate in their nests, merely sleeping in them for one night before moving on the next day. If we conclude that "a phylogenetic connection between the sleeping nest of the pongids [great apes] and the breeding nests of the lemurs cannot be constructed" (Hediger, 1977:180), we may be better to label the constructions with different names.

The second implication of nest-building in apes concerns the evolution of early hominins (Groves and Sabater Pi, 1985; McGrew, 1992; Sept, 1992, 1998). Considering other areas of strong overlap in great ape and human social systems (e.g. general size, subgrouping behavior, consortships, etc.) ape nesting behavior is seen by some as a means of addressing questions aimed at better understanding the transition *Homo* undertook from early foraging to later (and current) stable, subsistence strategies (Groves and Sabater Pi, 1985; Sept, 1992). Unfortunately, however, with no archaeological record of nest building, tracing the evolution of this behavior remains problematic, especially considering the role that climatic changes and human impact have had on chimpanzee resource accessibility in recent years (Sept, 1998). Potential indicators (i.e. comparative anatomy) remain though, and ethoarchaeology may prove to be a valuable method of linking extant primate behavior with potential fossilized evidence of what "home" or "camp" was for early humans (Hediger, 1977; Groves and Sabater Pi, 1985; Sept, 1992, 1998). Moreover, combining archaeological evidence and observation from the same chimpanzee site (e.g. Tai - Mercader et al., 2002) may provide insight into how behavior is reflected in the fossil record and, more importantly,

how potential ecological resources have varied over time. For those who study savanna chimpanzees and their evolved strategies for living in marginal habitats, this is important for learning about how habitat heterogeneity influences behavioral repertoires and patterns (Sept, 2002).

Thirdly, our learning about ape nesting behavior can provide strong evidence for not only cultural differences between ape communities (Baldwin et al., 1981; McGrew, 1992), but also demonstrate and reveal other phenomena such as tool use (Goodall, 1968; McGrew, 1992; McGrew et al., 2002), the extent to which some primates use mental maps (McGrew, 1992; Sept, 1998) or "distalward migration of conscious control" (Groves and Sabater Pi, 1985:45), the latter referring to the planned configurations of ape hand movements as sometimes seen in sign language and gesturing (Reynolds, 1981). Despite initial hesitancy to grant apes these higher processes simply based on nest building behaviors (Tuttle, 1986), the phenomenon has recently been summarized as, "the most pervasive form of object manipulation in the Pongidae" (Fruth and Hohmann, 1994:109), with each nest described as, "a skillful interweaving" (McGrew, 1992:210). If considered tool use, nest-building would be different than all other observed forms in that it (1) occurs daily, (2) is seen in all great ape species except humans, and (3) is characterized by different species (Fruth and Hohmann, 1994). Hediger (1977) appears to differentiate most primate nests from those of others mammals by suggesting differences in function and their importance to the territory, i.e. for primates, apes specifically, these constructions do not represent "fixed points" located in the center of a territory.

The final implication (and most relevant to the current study) of nest behavior in apes is the reflection it may be of behavior to an extreme habitat. If, for example, savanna chimpanzees are forced to disperse into small parties during the day in search of sufficient food and water sources (Chapter Five), then it is possible individuals will aggregate in larger nest parties to maintain group cohesion. I would predict clumped and larger nest parties during the mid to late dry season when resources force chimpanzees into greater daily dispersal patterns.

Great ape nesting behavior has not been a central focus at any of the established chimpanzee research sites (although see Fruth and Hohmann, 1994, 1996; Fruth, 1995;

Basabose and Yamagiwa, 2002). This can be interpreted for as due to various reasons. First, because apes are diurnal, nest building has been overshadowed by daily observations on social behavior (Fruth and Hohmann, 1996). Furthermore, because at most sites subjects have been provisioned (Nishida, 1968; Wrangham, 1974; Sugiyama, 1981, 1984; Goodall, 1986) or habituated well enough that researchers can use direct observation to study daily social behavior such as aggression (Boesch and Boesch-Achermann, 1989; Mitani and Watts, 1999; Wrangham, 1999; Watts, 2004), factors influencing social structure (see Chapter Two), and sex-specific relationships (Wrangham et al., 1992; Newton-Fisher, 1999; Pepper et al., 1999; Boesch and Boesch-Achermann, 2000; Watts, 2003). As a result, data on nesting have lagged. However, because savanna chimpanzees live in more marginal and open areas with a lower density of suitable trees for nesting (Pruetz, unpublished data), nesting patterns in these animals may be critical for us to understand how they use and depend on scarce resources. For example, Pruetz (pers. comm.) has suggested that almost 3% of all nests found at Fongoli are ground nests (Figure 6.1.), a seemingly high number for any chimpanzee community. Whether this phenomenon is an artifact of decreased predation pressure or lower available tree densities has not yet been determined, but its very presence may suggest another savanna chimpanzee adaptation. Moreover, with the recent attention being paid to cultural differences across chimpanzee communities (Whiten et al., 1999), the dynamics of nesting behavior in savanna communities, combined with the conservation implications of how these apes use on their arid environment, are in need of more attention at other established sites.

Constructing a Nest

Each individual weaned chimpanzee constructs a new nest every night (Figure 6.2.). Individuals begin constructing their own nest around the age of four (Fruth and Hohmann, 1996), and it is thought that this behavior is learned through imitation of kin and conspecifics (Bernstein, 1967; Watts and Pusey, 1993). That this construction ability is acquired quickly is not surprising considering the cognitive abilities of chimpanzees (Tomasello & Call, 1997; Matsuzawa, 1998). And whereas it appears that chimpanzees prefer constructing new nests each night, it is not unusual to find recent or old nests that have

Fig. 6.1. Example of a ground nest made by a Fongoli chimpanzee

Fig. 6.2. A fresh nest constructed within woodland habitat during the wet season (Photo courtesy of F. Stewart)

been reused, especially in areas where potential nesting trees occur at lower densities and where nests decompose more slowly (e.g. Fongoli - Pruetz et al., in prep; pers. observation). Nest construction typically lasts between one and five minutes (Goodall, 1962, 1986; Fruth and Hohmann, 1996), with individuals bending branches from reachable trees into a matrix that becomes the foundation of their nest. Chimpanzees also construct day nests, although these typically use fewer branches and require less construction time, therefore lacking the structure and foundation found in night ones (Goodall, 1962). It is not yet clear how often

they are made or the variables motivating their construction, but at Gombe Stream National Park in Tanzania, Goodall (1962) suggested that only one in eight individuals constructed them at all.

6.2 Factors Affecting Nesting Behavior

The factors that contribute to where chimpanzees (and other apes) sleep have generally eluded researchers. Early hypotheses addressing this topic suggested that, as in other apes (Schaller, 1961), chimpanzees show preferential nesting sites within their home range depending on specific habitat features (e.g. tree species, gradient of land, proximity to water, etc.) (Baldwin et al., 1982; Andersen et al., 1983; Kortlandt, 1992; Basabose & Yamagiwa, 2002), or in response to particular demographic and life history variables including age, sex, and cultural differences (Fruth & Hohmann, 1994, although see Brownlow et al., 2001). More recently, foci have centered on the relationship between nesting sites/behavior and, specifically, how nesting sites relate to seasonal changes in resource abundance (Furichi et al., 2001a; Basabose & Yamagiwa, 2002), with the aim of testing the long-held hypothesis that chimpanzees do not nest in feeding trees (Goodall, 1962). This hypothesis has been supported by data from bonobos *(Pan paniscus)*, who have been shown to nest in proximity (but not directly in) feeding trees to monopolize them early the next morning (Fruth, 1995; Fruth & Hohmann, 1996). Basabose and Yamagiwa (2002), however, found that chimpanzees at Tshibati, Kahuzi-Biega National Park, Democratic Republic of Congo, in fact, *prefer* nesting in fruiting trees used as food sources and that nest party size positively correlated with fruit abundance within those trees. Likewise, chimpanzee nest parties in Kalinzu Forest, Uganda, showed a significant positive relationship with fruiting seasons (Furichi et al., 2001a), further lending support to the idea that chimpanzee nest parties fluctuate in response to changing ecological variables.

Uses of nesting behavior for party size at Fongoli

Most studies on nesting behavior in chimpanzees have used the behavior as a means of censusing communities not yet habituated or well-known (Marchesi et al., 1995; Plumptre & Reynolds, 1996, 1997; Pruetz et al., 2002; Blom et al., 2003; Matthews and

Matthews, 2004). Some, however, have used the measure to indicate patterns in social behavior (Fruth & Hohmann, 1994; Fruth, 1995; Furuchi et al., 2001a, 2001b; Basabose and Yamagiwa, 2002). Like these latter studies, the current study attempted to use chimpanzee nesting behavior as an indicator of particular social dynamics, e.g. party size, as well as savanna chimpanzee adaptations to extreme ecological conditions (Moore, 1992). Fruth (1995) suggested that the difference between day and nest party size may indicate to what extent animals are congregating at night, i.e. if the difference between means was greater than 0, parties were considered tending towards fusioning, whereas a difference of less than 0 indicated parties tending towards fissioning, with the absolute distance from 0 denoting the intensity of such trends). Although nesting behavior in the apes may also reflect other social dynamics[2], the current study was not able to address such specific relationships within the Fongoli community, but rather compared day and nest mean monthly party size in relation to food distribution, something not yet studied extensively in savanna chimpanzees.

In the current study nesting party size was examined in two ways. First, data from Fongoli chimpanzee nesting behavior were compared to that of other chimpanzee study sites, both savanna and forested. Second, nesting party size was examined as it represented daily party size, for it is thought that savanna chimpanzees may aggregate at night more so than forest chimpanzee do in order to maintain social grouping cohesion, otherwise made difficult by a more open habitat (Hernandez, pers. comm.).

[2] Fruth (1995) noted that in bonobos *(Pan paniscus)*, nest location within a group accurately reflected patterns of social structure (high ranking individuals typically nested at the center of a party).

6.3 Methods

The current study focused on the Fongoli community of chimpanzees in southeastern Sénégal (12°55'N 16°02'W). This region has been characterized as a Sudanian-Guinean mosaic habitat, composed mainly of woodland-savanna, and broken up by large stretches of lunar-like plateau and pockets of gallery forest (Hunt and McGrew, 2002; McGrew et al., 1981). The village of Fongoli (Figure 5.4.) lies 6 km NW of the regional capital of Kédougou and <50 km SE of the Parc National du Niokolo Koba (PNNK), not far from the Malian (~ 85 km) or Guinean (~35 km) borders. Permission to conduct research in the area has been granted to Jill Pruetz by the Department du Eaux et Forets du Sénégal, as well as by local tribal leaders of the surrounding villages.

Study Site

The study area itself is a 50 km^2 region and contains three villages: the smallest (Fongoli) being home to <50 people and the largest (Djenji) <500 (pers. obs.). Between these villages much of the land is heavily disturbed by people from the encompassing villages and also those from Kédougou (Figure 5.1.), who have established agricultural fields throughout the area (Knutsen, 2003). Because the study period was limited to seven months, if and how often chimpanzees use uninhabited crop fields and whether party size was adjusted because of that could not be assessed. It is thought, however, that all animals typically avoid these rather open areas for the same reasons they avoid plateaus (predation and heat). Human presence is seen throughout the area during all months. Most hunters await potential game at valued water sources and appear to prefer warthog *(Phacochoreus aethiopicus)* and monkey *(Cercopithecus aethiops* and *Erythocebus patas)*, avoiding chimpanzee in response to cultural traditions (Clavette, 2003). Overall resource competition between humans and nonhumans is thought to be highest during late dry seasons when food and water availability are predictably low for all organisms (Duvall, 2000; Pruetz, 2002).

Study Subjects

Study subjects (Figure 6.3.) were individuals in the not yet fully-habituated, non-provisioned Fongoli community of chimpanzees in southeastern Sénégal. At the end of the current study, in December 2003, 16 adult individuals had been identified (10 males and 6 females). Combined with a largest single party observation of 22 individuals, Pruetz (unpublished data) has estimated a minimum community size of 26 individuals. Most chimpanzee encounters resulted in multiple contacts with a single party for a variable amount of time, although single sightings were not infrequent. Average distance from observer to chimpanzee party ranged from 10 meters to over 100 (N=67).

Fig. 6.3. Adult male chimpanzee at Fongoli

Flora and Fauna at Fongoli

Flora

For a discussion of the flora at Fongoli, see Chapter Four.

Fauna

Following Baldwin (1979), Table 6.1. lists other wildlife in the area and their relationship to chimpanzees. Other than other diurnal primates who will compete for high quality fruits (Kano, 1971; Sharman, 1981; Harrison, 1983), most large mammals are not thought to compete with chimpanzees for food sources, although all animals are predicted to compete heavily for water sources during the dry season.

TABLE 6.1 List of all known primates and small mammals observed at Fongoli during the study period

Scientific Name	Common Name	Relationship to Chimpanzee
Papio hamadryas papio	Guinea baboon	Competitor
Cercopithecus aethiops	Green monkey	Competitor; Prey
Erythrocebus patas	Patas monkey	Competitor
Galago senegalensis	Senegalese bushbaby	Prey
Mungus mungo	Banded mongoose	None
Hystrix crisatta senegalica	Crested porcupine	None
Viverra civetta	African civet	None
Genetta genetta	Common genet	None
Felis sylvestros libyca	African wild cat	None
Helioscirius gambianus	Gambian sun squirrel	Potential prey?
Xerus erythropus	Striped ground squirrel	Potential prey?
Phacochoerus aethiopicus	Warthog	none

Fig. 6.4. Guinea baboons *(Papio hamadryas papio)* in the PNNK seen here drinking from a water hole during the late dry season

Previous Chimpanzee Research in Sénégal

The last formal chimpanzee study began in Sénégal 1976 with the initiation of the Stirling African Primate Project (SAPP). Beginning a long-term research study at Mt. Assirik, in the PNNK (Figure 6.4.), the project's objectives included habituation of a community of chimpanzees within the Parc and collection of behavioral and ecological data

(Baldwin, 1979; McGrew et al., 1981; Tutin et al., 1983). The project lasted four years with data collected on, diet (McGrew et al., 1988), nesting (Baldwin et al. 1981), ranging (Baldwin et al., 1982), and social behavior (Tutin et al., 1983); habituation was never fully completed and the project consequently was aborted in 1979.

Fig. 6.5. Map of Sénégal, Kédougou is located in the southeast part of the country

Efforts to explore savanna chimpanzee socioecology, however, were renewed in this region in 2000 when Pruetz et al. (2002) initiated a survey comparing chimpanzee densities within and outside the PNNK's boundaries. Known as the Miami African Primate Project (MAPP), researchers found that chimpanzee densities had risen within the Parc's boundaries since the SAPP work of the late 1970s. More importantly, results indicated that chimpanzee densities were possibly as high as 0.09 individuals/km^2 outside the Parc (compared to 0.13 individuals/km^2 within the Parc) where chimpanzees would have to compete with local villagers for scarce water and food sources (Pruetz, 2002; Pruetz et al., 2002; Knutsen, 2003). Densities were lowest in savanna areas (0.008) and highest in gallery forest patches (0.03). Further investigation found that chimpanzees in this region of Sénégal are rarely hunted and

co-exist with people of the surrounding villages. As a result of these findings, a long term project was established in 2001 in and around the village of Fongoli, 4 kilometers south of Kédougou (Figure 6.5.), within the Tomboronkoto region. The project's current objectives are to habituate a community of chimpanzees while also examining aspects of human-chimpanzee competition for limited resources (Pruetz, 2002; Pruetz & Knutsen, 2002; Knutsen, 2003). Ultimately the project aims to examine the effect of savanna food resources on chimpanzee behavior and social organization.

Locating nests

Chimpanzee nests were located while researchers pursued evidence of chimpanzee presence (feeding remains, fecal remnants, Figures 6.6. and 6.7.). Local hunters, farmers, and other villagers encountered by researchers within the study area were often asked for

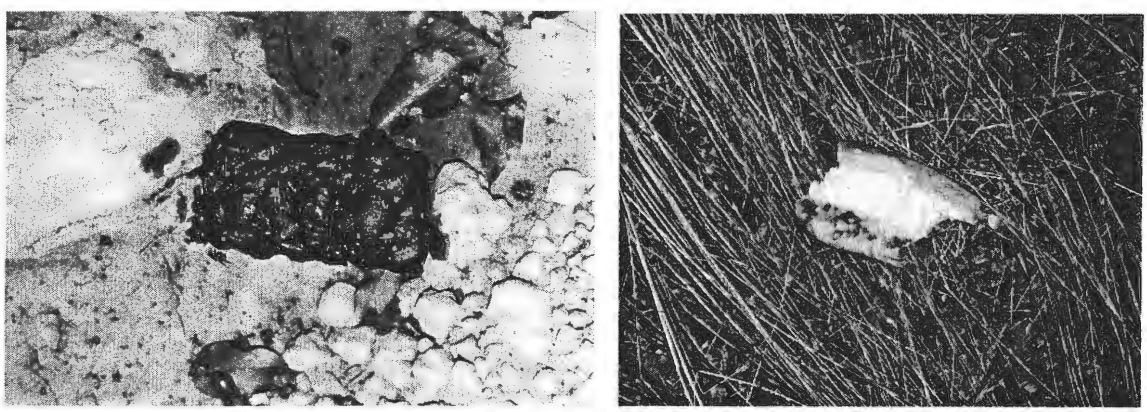


Fig. 6.6. and 6.7. On the left, a chimpanzee fecal, composed 95% of *Cissex* spp., while on the right, a feeding remain of *Afzelia africana* found along a chimpanzee trail (Photos courtesy of F. Stewart)

information (e.g. when the last time was and in what approximate area they heard or saw) regarding chimpanzees. Because chimpanzees call frequently when arriving and departing a nest site (Goodall, 1986), local people living within the study area regularly hear chimpanzee vocalizations when researchers are absent. Their suggestions were often used in accordance with predetermined areas needing surveying for chimpanzee activity.

When nest parties were located, a GPS point was recorded, as well as data on surrounding habitat, height of nests, nest trees, and distance between nests (i.e. nearest neighbor). This latter record will be used in analyses investigating habitat-specific

differences in nesting behavior (i.e. do savanna chimpanzees construct nests farther apart from each other than do forest chimpanzees?). Once a fresh nest was located, a 50 meter perimeter was estimated and researchers searched for other nests.

Analyses

Data on all chimpanzee nests found throughout the study were recorded, however only data recorded on fresh nests are considered in analyses regarding nesting party size. Student T tests examined the relationship between nest party size and definitions and habitat and sought to determine whether Fongoli chimpanzees aggregate in larger mean parties at night than during the day. This test was critical to assess potential behaviors savanna chimpanzees adapt to maintain strong social bonds in extreme ecological conditions. For instance, whereas it has been found that some apes aggregate in larger groups at night (Fruth & Hohmann, 1994, Figure 3), this phenomenon is not universal across study communities (Wrangham & Smuts, 1980) and has not yet been examined in any savanna communities. The current study used data on monthly mean daily party size and nesting party size to examine if this behavior was characteristic of the Fongoli community. Criteria for fresh nests were adopted from two sources and subsequently compared. The first followed recent studies (Fruth, 1995; Marchesi et al., 1995), in defining a fresh nest as that of one consisting of only green and no wilted leaves (Tutin and Fernandez, 1984), whereas the second used included the former definition, but added that a evidence fresh fecal or urine remains must be present under or near the nest, indicating recent chimpanzee presence there (from Pruetz et al., 2002). These two definitions were compared to examine if, as in day party size, the chosen definition affects results. This type of relationship is important when results are compared across study sites and years.

6.4 Results

Fresh nest parties were found on 37 different occasions throughout dry, transitional, and wet seasons. Most nest groups were located while searching daily for chimpanzee parties, although farmers living in the surrounding areas often volunteered information regarding vocalizations heard during the previous night. In this way not all nest groups were found opportunistically. Similar to daily parties observed, nest groups consisting of only a single nest were the most frequently found (N=14, 37.8%) with the largest single group of nests located being 16 (see Figure 6.8.)[3]. Only on six occasions were nest groups of greater than ten nests observed. Mean fresh nest group size using Pruetz et al. (2002)'s definition was 4.9 (SD = 4.53, N=37) as compared to 5.5 when Tutin and Fernandez's (1984) was used (see below).

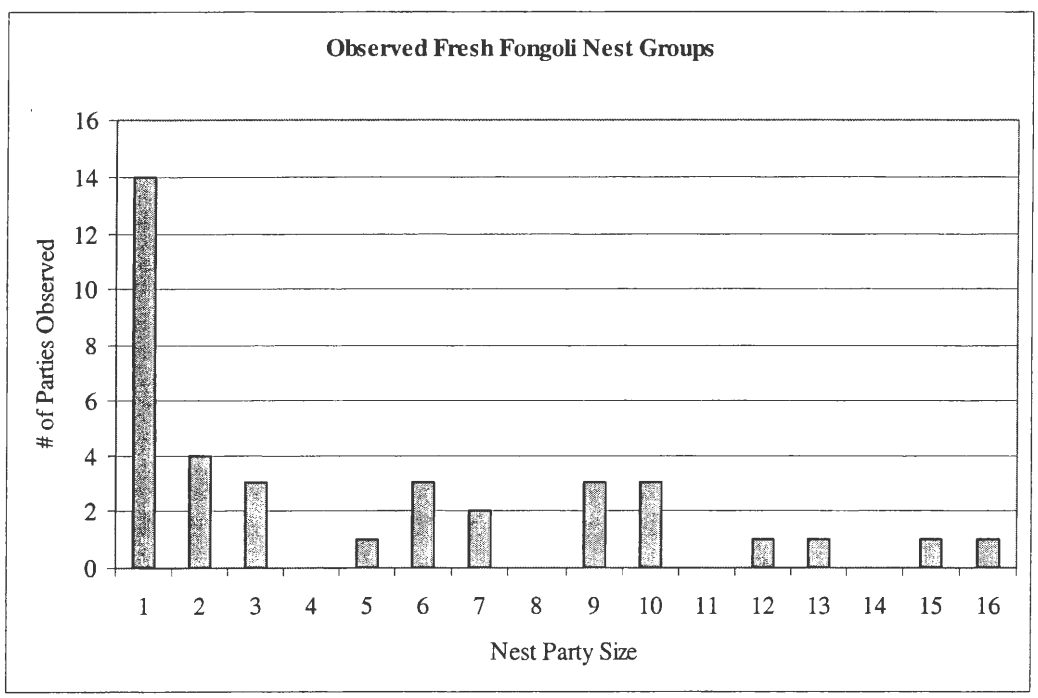


Fig. 6.8. Fresh nest party sizes observed (N=37) over the course of the study period. 38% (14/37) of all fresh nest groups found were single nest parties

[3] These data use Pruetz et. al.'s (2002) definition for 'fresh' nest

Defining a single nest group

On four occasions it was unclear how many nests belonged to the same group. Like daily party, nesting party has yet to be universally, operationally defined, with some researchers dubiously defining a group as clusters, presumed to be built at the same time, that are "close together" with a "similar...degree of decomposition" (Fruth and Hohmann, 1994:119). A previous study facing this problem concluded that some nest groups were composed of different "units", with ecological barriers (e.g. bushes or large trees) separating smaller nest subparties (Groves and Sabater Pi, 1985). This was never seen at Fongoli and is not expected considering the overall openness of the region (pers. obs.). No other known study has sought to establish criteria for how to determine a nesting party. As a result, researchers arbitrarily chose ~50 m as the distance between neighboring nests that could be considered in a single group. As with daily party size, selecting an arbitrary distance by which to separate nesting parties is problematic. Auditory, visual, or other cues may allow individuals to remain in contact throughout the night and consequently coordinate behavior. For example, Moore (pers. comm.) has suggested that chimpanzees in the Tongwe East Forest Reserve, western Tanzania, may sleep on hillsides to take advantage of better acoustic dynamics and consequently, be able to communicate better once nested. Groves and Sabater Pi (1985:26), after comparing nest groups from various sites, concluded that, "the greater dispersal of the nests may reflect the nature of the substrate, or may relate to the less cohesive nature of the society." Both of these are critical in influencing how a nest group is defined, both in tropical forest and savanna regions alike. Despite earlier studies addressing nesting patterns as a expression of social cohesion (Fruth, 1995), the current study centered instead on how these nest parties may be an indirect reflection of the distribution of food and water resources.

Habitat

Figure 6.9. shows mean nest party size in four different habitats. Although the only 11% (4/37) of nests were found in gallery patches, mean party size was found to be highest in these areas, nearly 63% larger than the next largest (woodland). Most nest groups were found in marigot areas, where water is abundant throughout the wet season.

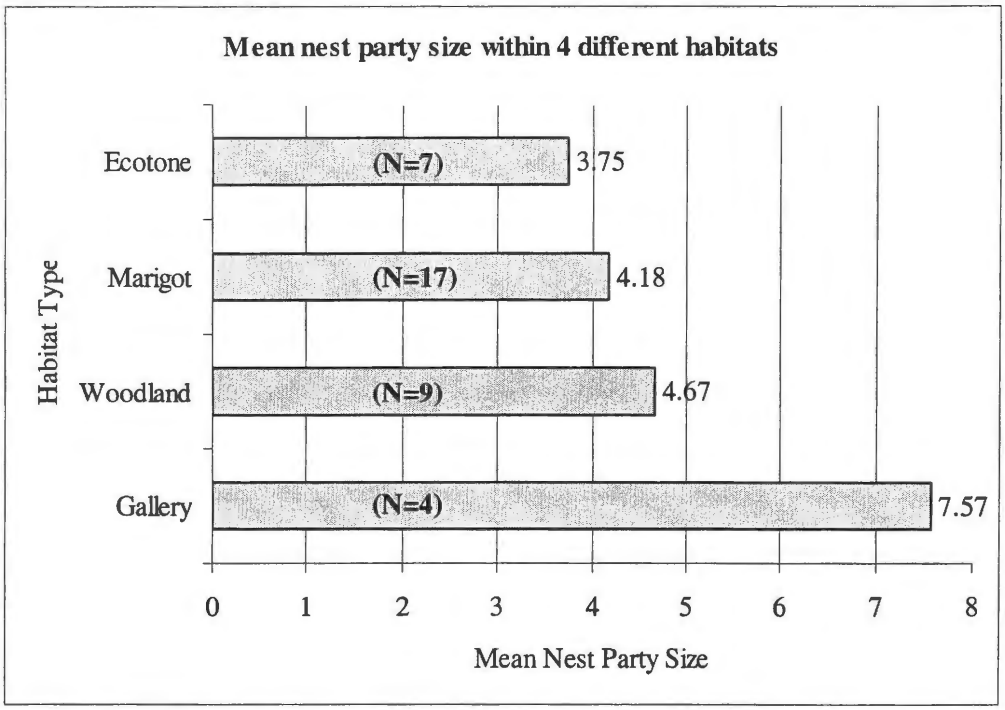


Fig. 6.9. Mean nest group size as found in each of four different habitat types. Gallery forest patches hosted significantly larger parties than any other habitat type

Definition Dilemma

Just as definitions of daily party size were compared in Chapter Five, a similar comparison was made regarding the different ways researchers define a 'fresh' nest. Tutin and Fernandez's (1984:317) original criteria suggested four different categories for nests (fresh, recent, old, and rotten) and has since formed the established method for characterizing chimpanzee (and gorilla) nests. Pruetz et al. (2002) later added to the 'fresh' definition the presence of a fresh fecal or urine sample under the nest, further substantiating the age of the nest. These two definitions were compared to investigate whether the definition chosen by the researcher would significantly affect the results reported. Of the 37 fresh nest groups that were found, 13 of the groups consisted of at least one nest that conformed to Tutin and Fernandez's (1984) original criteria for 'fresh', but lacked a fecal or urine sample underneath it. I conducted a Paired Student's T-test to look for differences between nest group definitions: those that included only fresh nests *with* fecals, and those that included all suspected fresh nests (i.e. all nests that conformed to Tutin and Fernandez's (1984), but not necessarily Pruetz et al.'s (2002) criteria). I found a significant difference between the two

definitions ($p<0.0001$). The mean size for those nest groups conforming to Tutin and Fernandez's definition was 5.5 (N=13), versus a mean of 4.9 (N=24) for those nests where only fresh fecal-nests were used. Figure 6.10. compares the data under both definitions.

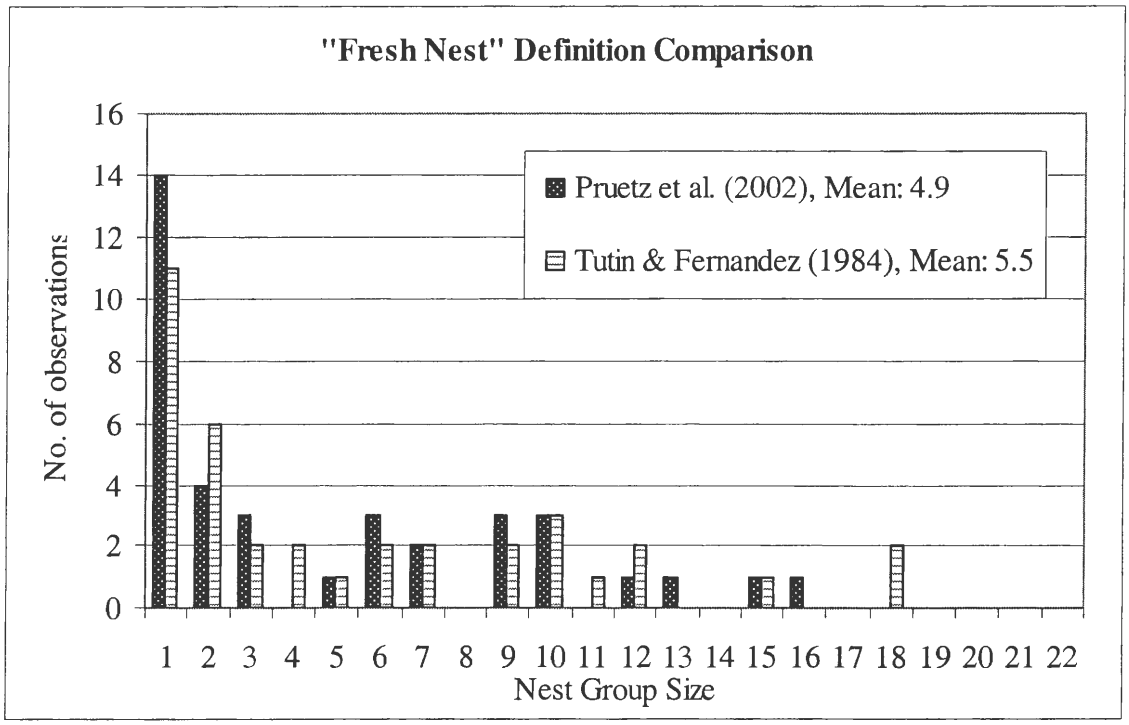


Fig. 6.10. Comparison of 'fresh' nest groups under definitions by Tutin and Fernandez (1984) and Pruetz et al. (2002).

Summary

As with daily party size (Chapter Five), the most frequently detected nest parties consisted of a single nest with the largest nest group (16) being almost as large as the largest observed day party (18). Mean nesting party size was found to be 5.5, nearly 30% larger than mean day party size (4.1), suggesting that Fongoli chimpanzees show strong fusion intensity (Fruth, 1995), the importance of which will be discussed below. Statistically significant differences were found when Tutin and Fernandez (1984)'s and Pruetz et al. (2002)'s definitions of a 'fresh' nest were compared and although small sample size prevented statistical analysis on the effect of habitat on nesting, trends indicate Fongoli chimpanzees prefer moist (marigot woodland and gallery forest patches) areas to construct night nests.

6.5 Discussion

Most studies that examine nesting behavior in chimpanzees do so in the attempt to reveal population densities (Kano, 1972; Baldwin et al., 1982; Marchesi et al., 1995; Plumtre and Reynolds, 1996, 1997; Pruetz et al., 2002) or habitat use (Baldwin et al., 1982; Pruetz et al., 2002), with only few aiming to use nesting patterns as an indirect means of addressing the dynamics of social behavior (Fruth, 1995) or cultural variation (Baldwin et al., 1981). Multiple factors are thought to influence nest-site selection in chimpanzees, from particular habitat types (Baldwin et al., 1981; Andersen et al., 1983; Sept, 1992; Brownlow et al., 2001) to fruit abundance (Furuchi et al., 2001a, b), to the particular features of individual trees (Sept, 1992; Fruth and Hohmann, 1994; Hashimoto, 1995), to topographical elements (Furuchi and Hashimoto, 2004). Along with predation pressure and seasonal distribution of foods, these features are all thought to influence nesting behavior across various habitat types and therefore can act as means of investigating savanna chimpanzee socioecology. Undoubtedly, direct observation of chimpanzee behavior is more reliable, and therefore preferred when asking questions about sociality. However, with no community of savanna chimpanzees yet fully habituated, indirect measures are a key strategy that researchers must invoke to better understand the dynamics and adaptations of animals living in these marginal areas. Likewise, studies examining activities such as nest building can elucidate causal differences in behavior between communities, e.g. ecological or cultural (Baldwin et al., 1981; McGrew, 1992).

There appear at least two ways to define 'fresh nest group': one (Pruetz et al., 2002) of which is more specific than the other (Tutin and Fernandez, 1984). Although the current study used the criteria from previous work at Fongoli (i.e. Pruetz et al., 2002), these two definitions showed significantly different results when compared, as seen with daily party size. (see Chapter Five). Removing or minimizing this variation is critical to understanding the proximate causes of behavioral differences.

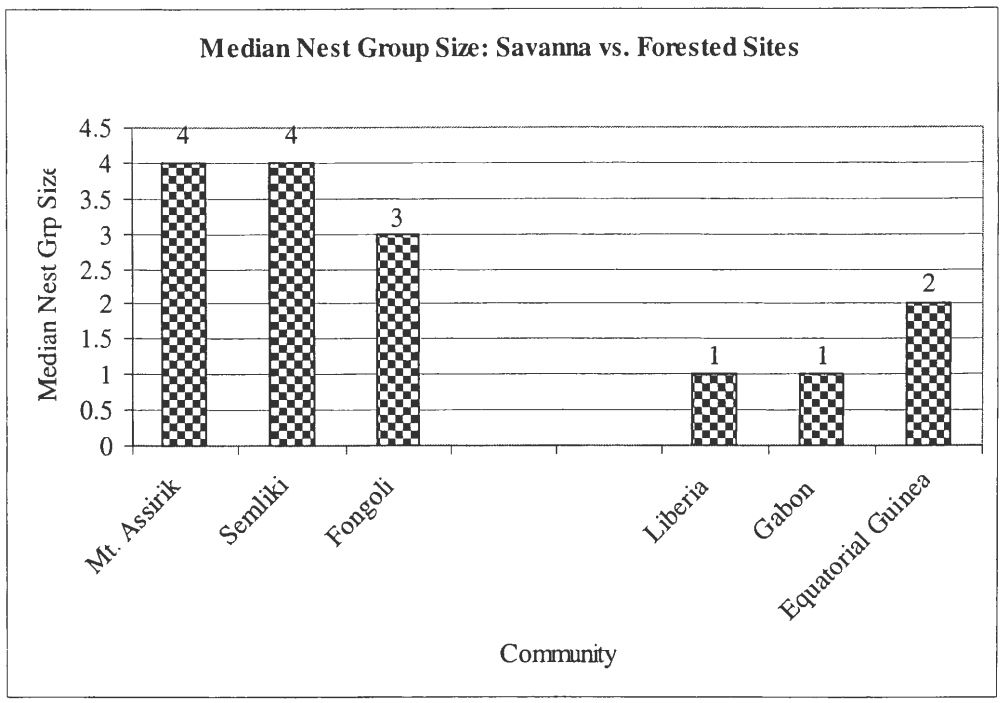


Fig. 6.11. Median nest party size compared over three different communities (Assirik: Baldwin et al., 1981; Semliki: Hunt and McGrew, 2002; Fongoli: current study; Forest site data from Fruth and Hohmann, 1994, Table 3).

Median nest size at Fongoli was three, similar to that seen at other savanna chimpanzee sites (see Figure 6.11.; Fruth and Hohmann, 1994, Table 3). Note here the distinct difference between median nest group size at savanna sites versus that of forested sites. It is not clear what factors contribute to this difference, although it remains possible that such larger grouping patterns at night reflect attempts by savanna chimpanzees to maintain contact otherwise not possible during daily travel (see below). Likewise, a comparison of results from the only other study of savanna chimpanzees (Figure 6.12.) indicates researchers most often found nest groups with only a single fresh nest. Mean nest party size at Fongoli was 5.5 (N=37), almost identical to that from Mt. Assirik (5.4 - Baldwin, 1979, see below). Chimpanzee nest groups were found to be larger during the wet season at Mt. Assirik (Baldwin, 1979), perhaps as a result of increased available nesting trees or because of potentially patchily distributed ripe fruit sources that triggered large aggregations of chimpanzees. A similar trend was also seen at Fongoli (see Figure 6.13.), where mean nesting party size steadily grew with the arrival of the wet season (June-November).

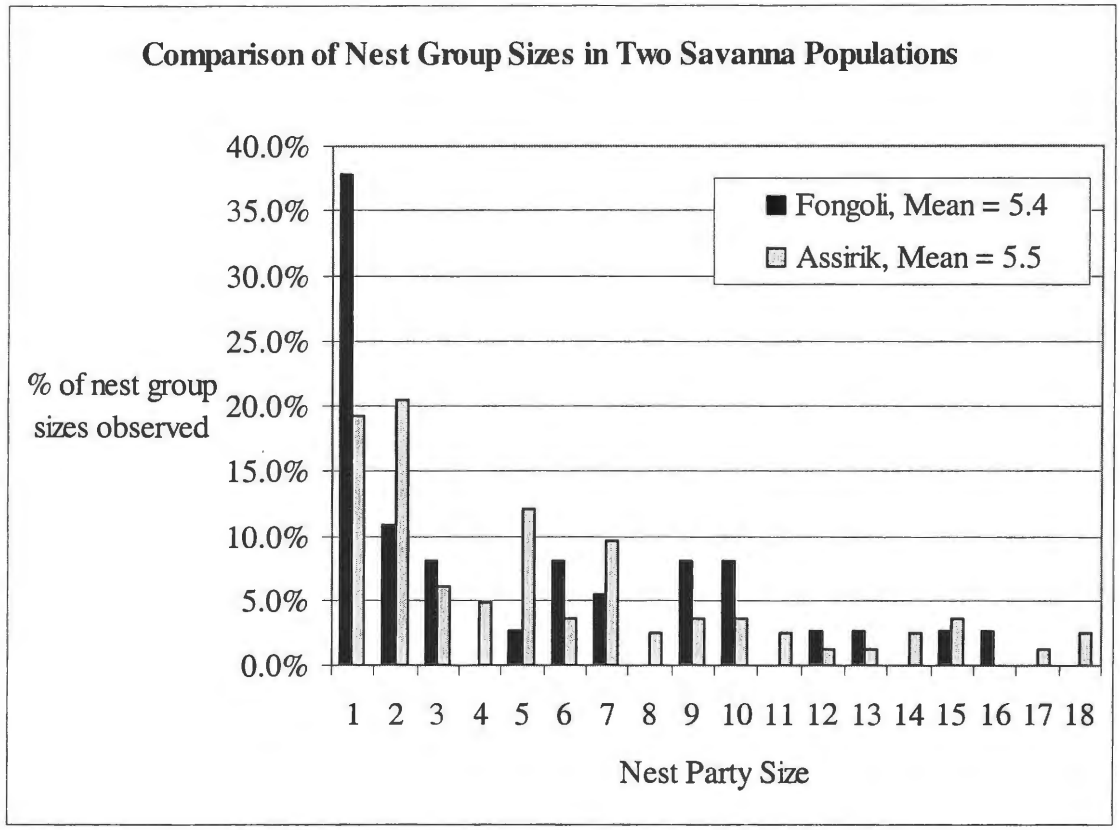


Fig. 6.12. Comparison of results from observed nest party sizes at Fongoli, Assirik (from Balwin et al., 1981, Figure 2).

Habitat

As in daily party dynamics, the role of habitat undoubtedly plays an important role in how we understand nest party sizes, especially if communication is assumed an important factor in allowing individuals to coordinate behavior (see above; Mitani and Stuht, 1998; Mitani et al., 1999). More open habitats like woodland and wooded grasslands should permit chimpanzee vocalizations to carry farther than closed canopy areas and as a result, allow chimpanzees to nest farther apart and still remain in contact. Baldwin et al. (1981) observed three significant effects of habitat on nesting behavior (nest height, number of nests per tree, and distance between nests) in three communities of chimpanzees in West Africa. Although the authors did not examine nest group size via different habitat types, they did find that the type of vegetation affected the number of nests per tree, just as the type of habitat seemed to affect the number of nests per group at Fongoli (Figure 6.9.). The results reported here,

however, do not follow earlier reports from Mt. Assirik (Baldwin, 1979), where chimpanzees appeared to nest more often in woodland than anywhere else. Marigot (see Chapter Four, Figure 4.4.), a type of woodland habitat that follows narrow streams was not considered a separate habitat type at Mt. Assirik during the SAPP work, but hosted more nest groups than any other habitat type in the current study.

At least one habitat type appeared to influence the size of chimpanzee nest parties at Fongoli. Although nests were found the fewest times in gallery forest patches (Figure 6.9.), the mean nest group size was the highest, unsurprising as these areas are characterized by higher canopy levels, more moisture, and increased shade, and consequently predicted to draw large aggregations of chimpanzees during the dry season when individuals seek refuge from soaring temperatures. These data, then, support those from Baldwin (1979), who concluded that the neighboring Mt. Assirik chimpanzees nest higher than any other known community. Whether individuals within the Fongoli community are nesting in gallery patches because of the higher available trees or for other reasons is not yet know, but is something to be explored in the future. Likewise, although the current study did not systematically examine seasonal differences in nesting behavior, it is predicted that individuals will more frequently nest in these areas during the dry season than during the wet one. What is surprising about these results, however, is the percentage of the total nest groups found in moist (marigots, gallery, ecotone) areas (28/37 = 77%). Known for providing permanent shade and water sources deep into the dry season, these areas refuge from extreme temperatures in the mid to late dry season. The sudden and extreme decline in mean nest group size in October may be a result of a brief dry spell where no rain fell for ~3 weeks (pers. obs.). If chimpanzees were responding to water availability, they may have had to disperse more widely to find reliable sources.

An increase in the construction of ground nests is also thought to be a result of the savanna mosaic. Although ground nests (Figure 6.1.) made up less than 1% of total nests found in the current study, they are predicted to deteriorate faster than arboreal nests and consequently, often elude researchers. There are two likely explanations for increased ground nesting at Fongoli. The first is a response to the extirpation of predators. Hunting pressure by local farmers and agricultural expansion has removed much of the habitat which at one time

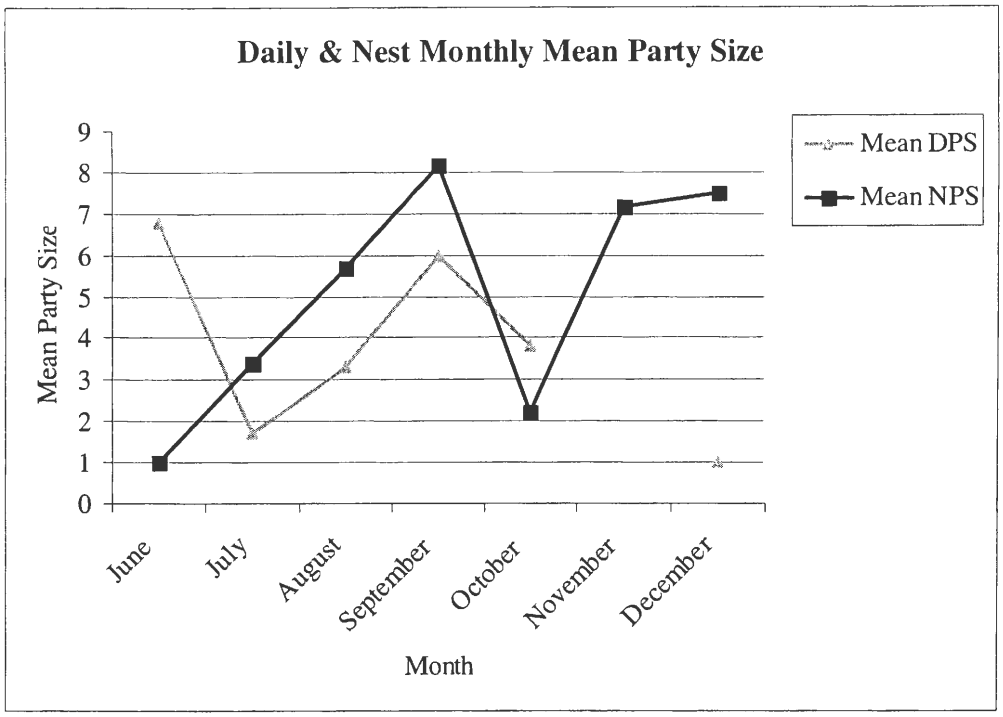


Fig. 6.13. Comparison of day and nest mean nest party size over the study period. Both means increased with the arrival of the wet season (June), but as the dry season approached and day party size decreased, nest party size increased.

may have protected some of the likely chimpanzee predators that naturally exist in southeastern Sénégal [e.g. lion *(Panthera leo),* leopard *(P. pardius),* spotted hyena *(Crocuta crocuta),* and African hunting dog *(Lyacon pictus)].* If these predators are no longer present, there would be little risk in sleeping on the ground. Although no ground nests were found in the SAPP work from Mt. Assirik (where predators are abundant), similar ground nest making was seen at Beni, Congo, where Kortlandt (1967) found 13% of all nests were constructed on the ground. Both sites, Fongoli and Beni, chimpanzees live close to human inhabitants are not hunted. This may allow them for such an otherwise high-risk behavior. Of more importance, however, is the second possibility: that chimpanzees at Fongoli are sleeping more on the ground because of reduced tree availability in certain areas. For many of the same reasons large predators no longer roam this region (human population rise, agriculture growth, urban expansion), much of the Sudanian-Guinean woodland has been converted to fields of peanuts, maize, and cotton (Knutsen, 2003). This, along with the increasing demand for wood used by locals for fuel and furniture, has thinned these woodlands, leaving wildlife

considerably less resources to use. This is perhaps another reason chimpanzees sleep most often in gallery patches and marigot strips.

Day versus nest party size

Like other studies, nest party size at Fongoli was used as an indirect means of answering other questions about chimpanzees: here, daily party size in a savanna community. Although previous research suggests that (1) nest groups may accurately reflect the relationship between individuals within the community (Fruth, 1995), (2) chimpanzees prefer smaller parties (Fruth and Hohmann, 1996), and (3) more familiar individuals nesting closer to each other (Fruth and Hohmann, 1996), none of these patterns are predicted to hold at Fongoli. The wide distribution of available food and water resources there are thought to force these chimpanzees to adjust their social behavior in order to optimally exploit what resources are accessible, while simultaneously maintaining the strong social bonds (especially between males) that characterize the genus *Pan.* Unlike those apes living in tropical forests, Fongoli individuals are thought to adapt both daily and sleeping behavior to their extreme environment (see below).

That chimpanzees may be aggregating at night in large parties is not a novel idea. For example, despite Goodall's (1962) early claim that chimpanzees nest near where they end their last feeding bout, she also suggested that the Gombe chimpanzees may have "nesting sites" where, we can infer, individuals prefer sleeping. Similar trends have been seen at other sites, including those in western Tanzania (Suzuki, 1969) and at Mt. Assirik, Sénégal (McGrew, pers. communication, cited in Sept, 1992:190). Sept (1992:190) has suggested that while other evidence of chimpanzee "ephemeral debris" may be insufficient to warrant the term "home bases" as used in the early hominin literature (Isaac, 1971; Leakey, 1971), some chimpanzee communities living in unambiguously dry regions exhibit "spatially redundant" behavior, similar to those of early hominins. Moore (1992) and Sept agree that this spatial redundancy may simply be an artifact of living in ecologically limited areas. Regardless of whether such behavior reflects the evolutionary origins of modern *Homo* subsistence patterns or merely ecological adaptations, evidence from Ishasa supports initial data seen at Fongoli.

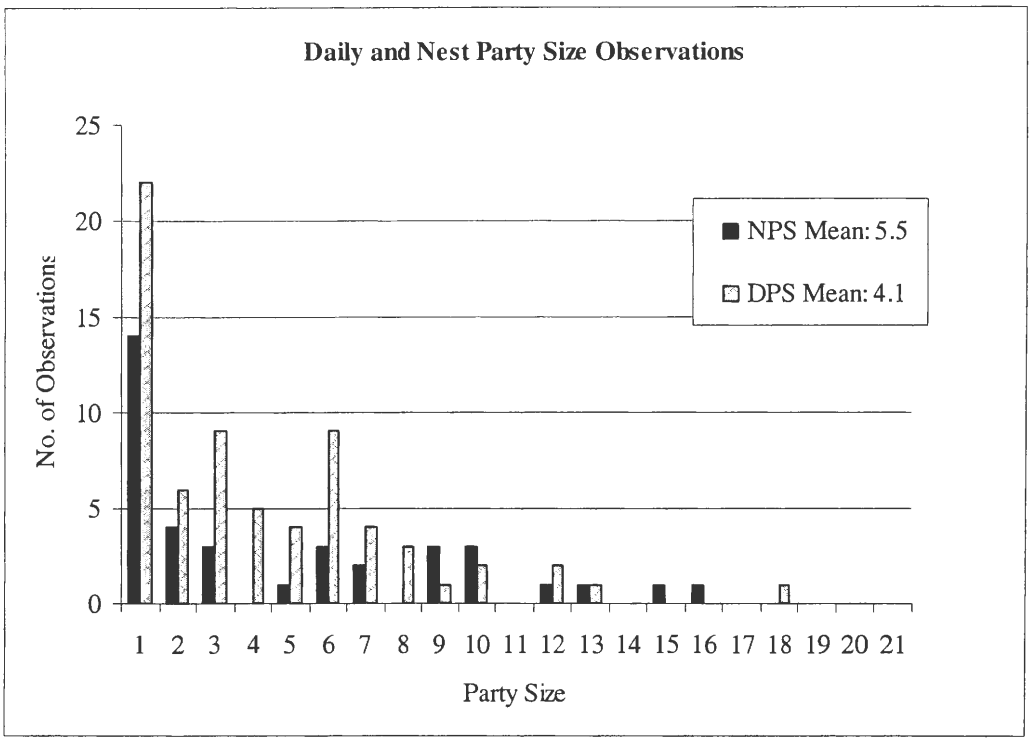


Fig. 6.14. Results from day party size (DPS) and nesting party size (NPS) means. Overall NPS was found to be 29% greater than overall DPS mean.

Figure 6.13. further demonstrates that at the onset of the dry season, day party size decreases while nest party size increases, lending weight to the notion that Fongoli chimpanzees are in fact aggregating in larger parties at night after dispersing into smaller ones during the day. These behavioral patterns should encourage us to reassess our overall understanding of chimpanzee fissioning and fusioning. Although *Ateles* was once thought to be the only other primate species to exhibit such a fluid grouping system, evidence now exists in other primates - orangutans (van Schaik, 1999), howling monkeys *(Alouatta palliata)* (Winkler, 2004) - and dolphins *(Sousa chinesis)* (Karczmarski, 1999). In none of these species, however, has anyone been able to quantify this social flexibility (Suarez, 2001), a potential means of comparing the behavior across taxa.

Conclusion

It may be suggested, then, that these chimpanzees prefer certain areas to aggregate at night after dispersing widely during the day (Hernandez, pers. comm.). Such large nest

groups may reflect their maintenance of social bonds, otherwise not reinforced by daily interactions. This has been seen in bonobos (Fruth and Hohmann, 1994), where groups exhibited a tendency to aggregate at night. The authors of that study suggested this was a fundamental difference in nesting behavior between the two *Pan* species. Results from the current study, however, indicate that this difference may not be species or environmentally-driven [bonobos live in moist, tropical rainforests in the southern Democratic Republic of Congo – not at all similar, at least ecologically, to savanna sites such as Fongoli (although see Lanjouw, 2002)]. To further investigate the causes behind such nesting patterns in the Fongoli community, future studies should address the distribution of these nest parties and the degree to which they are patchily distributed (i.e. I would predict large clumps of nests nonrandomly distributed throughout the homerange, especially during the mid-late dry season when food and water sources are more patchily distributed).

Summary

Results from the current study are compared here to those from the SAPP, conducted at neighboring Mt. Assirik, PNNK, in the late 1970s. In that study, Baldwin (1979) found nest parties to range in size from 1-18; at Fongoli the range was 1-16. Likewise, the mean nest party size over the course of the two year study was 5.4, almost identical to that reported at Fongoli (5.5, see Figure 6.14.). Moreover, at both sites daily party sizes (DPS) were found to be slightly smaller than nest party sizes (NPS) (Assirik: NPS = 5.4 vs. DPS = 4.6 - Baldwin, 1979; Fongoli: NPS = 5.5 vs. DPS = 4.1 – Fig. 6.14). Although the percentage of ground nests at Fongoli (3%) did not parallel that from some previous work (13% - Kortlandt, 1967), the Fongoli numbers may be underestimates considering the speed at which ground nests deteriorate and consequently elude researchers. The significance, however, of high numbers of ground nests cannot be under-emphasized. If, on the one hand, Fongoli chimpanzees are nesting on the ground as a response to the sudden and substantial elimination of terrestrial predators within their home range (pers. obs.), then such change provides evidence of immediate behavioral flexibility and adaptation. If, alternatively, these chimpanzees are nesting on the ground as a result of reduced nesting tree availability caused by increased cultivation of their home range, the implications for conservation and protection

of this area are great. Future research, then, should focus on (1) other behavioral changes adapted by chimpanzees in response to human population expansion and (2) overall human-chimpanzee competition in the region (Pruetz, 2002; Knutsen, 2003).

The data here suggest that the best way for the Fongoli community to cope with widely distributed food sources is to disperse into small day parties, probably traveling greater distances in search of sufficient food and water sources, while *reuniting* at night in larger groups. These reunions would, again, help to maintain social bonds and cohesion within the community Thus, although it was initially thought that mean nest party size would be similar to (i.e. a reflection of) daily party size, results suggest that Fongoli chimpanzees actually do nest in parties considerably larger (almost 30%) than daily party ones. The considerable difference between mean day party size (4.1) and nest party size (5.5) support this idea, providing evidence that chimpanzees living in these extreme conditions adapt their nightly grouping behavior to the distribution of critical ecological resources. It is predicted that as resources become more readily available (especially water), with more individuals able to travel together and maintain contact during the day, mean daily parties will increase while mean nest ones will decrease. Future research, then, should focus on whether or not this pattern remains across seasons, especially in light of the critical nature of resource distribution and abundance in dry, open, and arid 'extreme' savanna sites (McGrew et al., 1981; Kortlandt, 1983; Moore, 1992; Pruetz, 2002), as well as on the nature of fission fusion systems in chimpanzees and other species.

Sources

Andersen JA, Williamson EA, Carter J. 1983. Chimpanzees of Sapo Forest, Liberia: density, nests, tools and meat-eating. *Primates* 24:594-601.

Baldwin PJ. 1979. The natural history of the chimpanzee *(Pan troglodytes verus)* at Mt. Assirik, Sénégal. Unpublished Ph.D. thesis, Stirling: University of Stirling.

Baldwin PJ, Sabater Pi J, McGrew WC, Tutin CEG. 1981. Comparisons of nests made by different populations of chimpanzees *(Pan troglodytes). Primates* 22(4):474-486.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *Int' J of Primatol* 3(4):367-385

Basabose AK, Yamagiwa J. 2002. Factors affecting nesting site choice in chimpanzees at Tshibati, Kahuzi-Biega National Park: Influence of sympatric gorillas. *Int'l J of Primatol* 23(2):263-282.

Bernstein I. 1967. Response to nesting materials of wild born and captive born chimpanzees. *Anim Behav* 10(1):1-6.

Blom A, Almasi A, Heitkonig IMA, Kpanou JB, Prins HHT. 2001. A survey of the apes in the Dzanga-Ndoki National Park, Central African Republic: a comparison between the census and survey methods of estimating the gorilla *(Gorilla gorilla gorilla)* and chimpanzee *(Pan troglodytes)* nest group density. *African J of Ecology* 39:98-105.

Boesch C. 2002. Cooperative hunting roles among Tai chimpanzees. *Human Nature-Int Bios* 13(1):27-46.

Boesch CA, Boesch-Achermann H. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *Amer J of Phys Anthropol* 78:547-573

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution.* Oxford: Oxford University Press.

Brownlow AR, Plumptre AJ, Reynolds V, Ward R. Sources of variation in the nesting behavior of chimpanzees *(Pan troglodytes schweinfurthii)* in the Budongo Forest, Uganda. *American J of Primatol* 55 (1):49-55.

Charles-Dominique P. 1977. *Ecology and Behaviour of Nocturnal Primates: Prosimians of Equatorial West Africa.* New York City: Columbia University Press.

Clavette K. 2003.Conservation through Folklore: Ethnoprimatology in Southeastern Sénégal. Unpublished MA Thesis: Northern Arizona University.

Duvall CS. 2000. Important habitat for chimpanzees in Mali. *African Study Monographs* 21(4):173-203.

Fietz J. 1999. Monogamy as a rule rather than exception in nocturnal lemurs: the case of the fat-tailed dwarf lemur, *Cheirogaleus medius*. *Ethology* 105(3):259-272.

Fruth B. 1995. Nests and nest groups in wild bonobos *(Pan paniscus)*: Ecological and behavioural correlates. Aachen: Verlag Shaker.

Fruth B, Hohmann G. 1994. Comparative analysis of nest-building behavior in chimpanzees and bonobos. In: Wrangham RW, McGrew WC, de Waal FBM, Heltne PG, editors, *Chimpanzee Cultures,* Cambridge: Harvard University Press. p 109-128.

Fruth B, Hohmann G. 1996. Nest building behavior in the great apes: The great leap forward?, In: McGrew WC, Marchant L, Nishida T, editors, *Great Ape Societies,* Cambridge: Cambridge University Press. p 225-240.

Furuichi T, Hashimoto C, Tashiro Y. 2001a. Extended application of a marked-nest census method to examine seasonal changes in habitat use by chimpanzees. *Int'l J of Primatol* 22(6):913-928.

Furuichi T, Hashimoto C, Tashiro Y. 2001b. Fruit availability and habitat use by chimpanzees in the Kalinzu Forest, Uganda: Examination of fallback foods. *Int'l J of Primatol* 22(6):929-945.

Furuchi T, Hashimoto C. 2004. Botanical and topographical factors influencing nesting-site selection by chimpanzees in Kalinzu Forest, Uganda. *Int'l J of Primatol* 25(4):755-765.

Goodall J. 1962. Nest building behavior in the free ranging chimpanzee. *Ann. NY Acad Sci* 102:455-467.

Goodall J. 1986. *The Chimpanzees of Gombe: Patterns of Behavior.* Cambridge: The Belknap Press of Harvard University.

Groves CP, Sabater Pi J. 1985. From ape's nest to human fix point. *Man* 20:22-47.

Hashimoto C.1995. Population census of the chimpanzees in the Kalinzu Forest, Uganda – comparison between methods with nest counts. *Primates* 36(4):477-488.

Hediger H. 1977. Nest and home. *Folia Primatolgica* 28:170-187.

Isaac G. 1971. The diet of early man: aspects from archaeological evidence from Lower and Middle Pleistocene sites in Africa. *World Archaeology* 2:278-289.

Karczmarski L. 1999. Group dynamics of humpback dolphins *(Sousa chinensis)* in the Algoa Bay region, South Africa. *J Zoo* 249:283-293.

Knutsen PG. 2003. Threatened existence: *Saba senegalensis* in southeastern Senegal. Unpublished MA thesis, Ames: Iowa State University.

Kortlandt A.1967. Experimentation with chimpanzees in the wild. In: stark D, Schneider R, Kuhn HJ, editors, *Neue Ergebnisse der Primatologie*, Sttugart: Fischer.

Kortlandt A. 1992.On chimpanzee dormitories and early hominid home sites. *Current Anthropology* 33(4):399-401.

Lanjouw A. 2002. Behavioral adaptations to water scarcity in Tongo chimpanzees. In: Boesch C, Hohmann G, Marchant LF, editors, *Behavioural Diversity in Chimpanzees and Bonobos,* Cambridge: Cambridge University Press. 52-60.

Leakey M.D. 1971. Olduvai Gorge. Volume 3. Cambridge: Cambridge University Press.

Marchesi P, Marchesi N, Fruth B, Boesch C. 1995. Census and distribution of chimpanzees in Cote d'Ivoire. *Primates* 36(4):591-607.

Martin RD. 1975. The bearing of reproductive behavior and ontogeny on strepsirhine phylogeny. In: Luckett WP, Szalay FS, editors, *Phylogeny of the Primates,* New York: Plenum Press.

Matsuzawa T. 1998. Chimpanzee cognition: A comparative cognitive perspective. In: Greenberg G, Haraway MM, editors, *Comparative Psychology,* New York & London: Garland Publishing, Inc. p 360-375.

Matthews A, Matthews A. 2004. Survey of gorillas *(Gorilla gorilla gorilla)* and chimpanzees *(Pan troglodytes troglodytes)* in Southwestern Cameroon. *Primates* 45(1):15-24.

McGrew WC. 1992. *Chimpanzee Material Culture*: Cambridge University Press: Cambridge.

McGrew WC, Tutin CEG, Baldwin PJ. 1979. Chimpanzees, tool, and termites – cross cultural comparisons of Senegal, Tanzania, and Rio Muni. *Man* 14(2):185-214.

McGrew WC, Baldwin PJ, Tutin CEG. 1981. Chimpanzees in a hot, dry and open habitat: Mt. Assirk, Sénégal, West Africa. *J of Human Evolution* 10:227-244.

McGrew WC, Baldwin PJ, Tutin CEG. 1988. Diet of wild chimpanzees *Pan troglodytes verus)* at Mt. Assirik, Sénégal: I. Composition. *American J of Primatol* 16:213-226.

McGrew WC, Baldwin PJ, Marchant LF, Pruetz JD, Scott SE, Tutin CEG. 2002. Ethoarchaeology and elementary technology of unhabitutated chimpanzees at Assirik, Sénégal. *Paleoanthropology* 1:1-20.

Mercader J, Panger M, Boesch C. 2002. Excavation of a chimpanzee stone tool site in the African rainforest. *Science* 296(5572):1452-1455.

Mitani JC, Stuht J. 1998. The evolution of nonhuman primate loud calls: Acoustic adaptation for long-distance transmission. *Primates* 39(2):171-182.

Mitani JC, Watts DP. 1999 Demographic influences on the hunting behavior of chimpanzees. *American J of Phys Anthropol* 109(4):439-454.

Mitani JC, Watts DP, Muller MN. 2002. Recent developments in the study of wild chimpanzee behavior. *Evol Anthropol* 11(1):9-25.

Moore JJ. 1992. Comment. *Current Anthropology* 183(2): 187-207.

Naughton-Treves L, Mena JL, Treves A, Alvarez N, Radeloff VC. 2003.Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Cons Bio* 17(4):1106-1117.

Newton-Fisher NE 1999. Association by male chimpanzees: A social tactic. *Behaviour* 136:705-730.

Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.

Nissen HW. 1931. A field study of the chimpanzee. Observations of chimpanzee behavior and environment in Western French Guinea. *Comp Psych Mono* 8:1-122.

Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *Int'l J of Primatol* 20(5):613-632.

Plumptre AJ, Reynolds V. 1997. Nesting behavior of chimpanzees: Implications for censuses *Int'l J of Primatol* 18(4):475-485.

Plumtre D, Reynolds V. 1996. Censusing chimpanzees in the Budongo Forest, Uganda. *Int'l J Primatol* 17:85-99.

Pruetz JD. 2002. Competition between savanna chimpanzees and humans in southeastern Sénégal. *Amer J Phys Anthropol* 128-128 Suppl. 34 2002.

Pruetz JD, Knutsen P. 2003. Scrambling for a common resource: Chimpanzees, humans, and *Saba senegalensis*, in southeastern Sénégal. *Amer J Phys Anthropol* 172-172 Suppl. 36

Pruetz JD, Marchant LF, Arnot J, McGrew WC. 2002. Survey of chimpanzees *(Pan troglodytes verus)* in southeastern Sénégal. *American J of Primatol* 58:35-43.

Reynolds PC. 1981. *On the Evolution of Human Behavior.* Berkeley: University of California Press.

Sall M. 2000. *Atlas du Senegal.* Paris: Les Editions J.A.

van Schaik CP. 1999. The socioecology of fission-fusion sociality in orangutans. *Primates* 40(1):69-86.

Sept J. 2002. Chimpanzees on the edge: The implications of chimpanzee ecology in "savanna" landscapes for hominid evolution. In: Contreras JM, Véa JJ, editors, *Primates: Evolucion, Cultura Y Diversidad,* p 51-68.

Sept J. 1992. Was there no place like home? A new perspective on early hominid archaeological sites from the mapping of chimpanzee nests. *Current Anthropology* 33(2):187-207.

Sept J. 1998. Shadows on a changing landscape: Comparing nesting patterns of hominids and chimpanzees since their last common ancestor. *American J of Primatol* 46(1):85-101.

Stanford CB. 1995. The influence of chimpanzee predation on group-size and antipredator behavior in red colobus monkeys. *Animal Behaviour* 49(3):577-587.

Stanford CB. 1998. *Chimpanzee and Red Colobus: The Ecology of Predator and Prey.* Cambridge, Ma: Harvard University Press.

Stanford CB. 1999. *The Hunting Apes: Meat-eating and the Origins of Human Behavior.* Princeton: Princeton University Press.

Suarez SA. 2001. Quantifying fission-fusion and social dynamics in free ranging spider monkeys *(Ateles belzebuth belzebuth). Amer J of Anthropol* 145-146 Suppl. 32.

Sugiyama Y. 1981. Observations on the population dynamics and behavior of wild chimpanzees at Bossou, Guinea, in 1976-1980. *Primates* 22(4):435-444.

Sugiyama Y. 1984. Population dynamics of wild chimpanzees at Bossu, Guinea, between 1976-1983. *Primates* 25(4):391-400.

Tomasello M, Call J. Editors, 1997. *Primate Cognition.* Oxford: Oxford University Press.

Tutin CEG, Fernandez M. 1984. Nationwide census of Gorilla *(Gorilla g. gorilla)* and chimpanzee *(Pan t. troglodytes)* populations in Gabon. *American J of Primatol* 6:313-336.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

Tuttle RH. 1986. *Apes of the World.* New Jersey: Noyes.

Watts DP. 2003. Male dominance rank and mating success in an extremely large chimpanzee community at Ngogo, Kibale National Park. *American J of Phys Anthropol*: 221-221 Suppl. 36.

Watts DP. 2004. Intracommunity coalitionary killing of an adult male chimpanzee at Ngogo, Kibale National Park, Uganda. *Int'l J of Primatol* 25(3):507-521.

Watts DW, Pusey AE. 1993. Behavior of juvenile and adolescent great apes. In: Pereira ME, Fairbanks LA, editors, *Juvenile Primates,* Oxford: Oxford University Press. p 148-167.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. *Nature* 399(6737):682-685.

Wilson ML, Wallauer WR, Pusey AE. 2004. New cases of intergroup violence among chimpanzees in Gombe National Park, Tanzania. *Int'l J of Primatol* 25(3):523-549.

Winkler LA. 2000. Patterns of fission-fusion social organization in the mantled howling monkey *(Alouatta palliata)* in Nicaragua. *Amer J Phys Anthropol* 324-325 Suppl. 30.

Wrangham RW. 1974. Artificial feeding of chimpanzees and baboons in their natural habitat. *Animal Behavior* 22:83-93.

Wrangham RW. 1999. Evolution of coalitionary killing. *Yearbook of Phys Anthropol* 42:1-30.

Wrangham RW, Clark AP, Isabirye-Basuta G. 1992. Female social relationships and social organization of Kibale Forest chimpanzees. In: Nishida T, McGrew WC, Marler P, Pickford M, de Waal FBM, editors, *Topics in Primatology Vol. 1, Human Origins,* Tokyo: University of Tokyo Press. p 81-98.

Wrangham RW, Smuts BB. 1980. Sex differences in the behavioural ecology of chimpanzees in the Gombe Stream National Park, Tanzania. *J Reprod Fert* 28:13-31.

Wright PC. 1999. Lemur traits and Madagascar ecology: Coping with an island environment. *Yearbook Phys Anthropol* 42:31-72.

Chapter Seven: Summary and conclusions

The origins of diversity seen in chimpanzee behavior have long been a focus of primatologists (McGrew et al., 1979; McGrew, 1992; Whiten et al., 1999; Boesch et al., 2002). With populations of these apes found across the central belt of Africa, variations in the type of habitat in which they live and the nature of their competitors will undoubtedly cause behavioral differences among communities. The current study sought to explore if and how a population of savanna chimpanzees in southeastern Sénégal adapts their grouping behavior, here daily and nesting party size, to widely distributed food sources.

Even before attempting to unravel the many factors contributing to how chimpanzees maintain their fluid social system, merely defining that system may prove more difficult than initially thought. Studies now ongoing in more open, savanna habitats demonstrate the danger of assuming that one study's 'party' is the same as another's. That is, definitions based on arbitrary distances between individuals or ecologically-influenced faculties (e.g. auditory/visual contact) are typically not appropriate for all sites. For example, chimpanzees at Fongoli, on average, can easily see and hear considerably farther than those individuals living in moist, tropical forests (pers. obs.). Pepper et al.'s (1999) observation that these animals move in "amoeba-like" formations with no real constant shape, while accurate, likewise fails to help us standardize definitions. More thorough descriptions of the dynamics involved in chimpanzee 'parties' (i.e. spatial-temporal associations) may be necessary if researchers are to better understand this fission-fusion phenomenon.

It was hypothesized that the Fongoli community would form smaller mean parties than other, forest-dwelling populations. Mean party size for the seven month study was found to be 4.1, although is expected to change seasonally like at other sites (Wrangham, 1977; Boesch and Boesch-Achermann, 2000; Mitani et al., 2002; although see Baldwin, 1979; Tutin et al., 1983). To that extent, the fact that most of the data for this study were collected during the wettest months of the year (June-October) suggests that this number is the upper range of party size and that a more comprehensive study would produce a lower mean. Previous to this study, in fact, Pruetz, in initial years of study, had calculated mean party size

for this community to be 3.1. In the only other available data on savanna chimpanzee party size, Baldwin (1979) observed mean party size to be 4.6 with no seasonal differences in her study of a population of chimpanzees at Mt. Assirik, Sénégal. Moreover, Tutin et al. (1983) observed that during times of food and water scarcity, individuals from this same community retreated to the periphery of their range, suggesting increased travel for them to find sufficient resources. In following Chapman and Chapman (2000) and Janson and Goldsmith (1995), these animals should then form smaller groups to travel more efficiently. Similar patterns are thought to exist at Fongoli, with late dry season resources being widely dispersed. If such is the case, I predict smaller daily parties for chimpanzees during these drier months (February-May).

If Fongoli chimpanzees are forming smaller parties in response to scarce resources, we must ask how they are able to sustain the high degree of contact necessary in maintaining the social relationships that defines this species (Goodall, 1968; Nishida, 1968)? Although it was hypothesized that nest party size would accurately reflect day party size, results from the current study suggest that these chimpanzees may be aggregating in larger parties at night. Hernandez (pers. comm.) also suspects this type of grouping pattern in a community of chimpanzees at Ugalla, Tongwe Forest Reserve, western Tanzania. Nesting behavior would then be remarkably different from forest-dwelling chimpanzees, where Fruth (1995) found it to often accurately reflect the social dynamics of that community (i.e. dominance hierarchy, alliances). In the savanna examples above, nesting behavior, instead, may be used as a means of strengthening bonds otherwise not maintainable while traveling great distances in small parties during the day. Future studies that focus on the seasonal distribution of these nest groups and their size will shed light on this idea. It is predicted that nest groups will be larger during the late dry season when critical food and water sources are more widely distributed and chimpanzees are forming smaller daily subgroups to forage.

Sources

Baldwin PJ. 1979. The natural history of the chimpanzee *(Pan troglodytes verus)* at Mt. Assirik, Senegal. Unpublished Ph.D. thesis, Stirling: University of Stirling.

Baldwin PJ, McGrew WC, Tutin CEG. 1982. Wide-ranging chimpanzees at Mt. Assirik, Sénégal. *International J of Primatol* 3(4):367-385

Boesch CA, Boesch-Achermann H. 2000. *The Chimpanzees of the Tai Forest: Behavioural Ecology and Evolution*. Oxford: Oxford University Press.

Boesch C, Marchant LF, Nishida T. Editors, 2002. *Behavioural Diversity in Chimpanzees and Bonobos*. Cambridge: Cambridge University Press.

Chapman CA, Chapman LJ. 2000. Determinants of group size in primates: The importance of travel costs. In: Boinski S, Garber PA, editors, *On the move: How and why animals travel in groups,* Chicago and London: University of Chicago Press. p 24-42.

Fruth B. 1995. Nests and nest groups in wild bonobos *(Pan paniscus)*: Ecological and behavioural correlates. Aachen: Verlag Shaker.

Goodall J. 1968. Behaviour of free-ranging chimpanzees of the Gombe Stream Area. *Animal Behaviour Monograph* 1:163-311.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. *Behav Ecol* 6:326-336.

McGrew WC. 1992. *Chimpanzee Material Culture*: Cambridge University Press: Cambridge.

McGrew WC, Tutin CEG, Baldwin PJ. 1979. Chimpanzees, tool, and termites – cross cultural comparisons of Sénégal, Tanzania, and Rio Muni. *Man* 14(2):185-214.

Mitani JC, Watts DP, Lwanga JS. 2002. Ecological and social correlates of chimpanzee party size and composition. In: Boesch C, Hohmann G, Marchant L, editors, *Behavioural Diversity of Chimpanzees and Bonobos*, Cambridge: Cambridge University Press. p 102-111.

Nishida T. 1968. The social group of wild chimpanzees in the Mahale Mountains. *Primates* 9:167-224.

Pepper JW, Mitani JC, Watts DP. 1999. General gregariousness and specific social preferences among wild chimpanzees. *International J of Primatol* 20(5):613-632.

Tutin CEG, McGrew WC, Baldwin PJ. 1983. Social organization of Savanna-dwelling chimpanzees, *Pan troglodytes verus*, at Mt. Assirik, Sénégal. *Primates* 24(2):154-173.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C. 1999. Cultures in chimpanzees. *Nature* 399(6737):682-685.

Wrangham RW. 1977. Feeding behavior in chimpanzees in Gombe National Park, Tanzania. In: Clutton-Brock TH, editor, *Primate Ecology*, London: Academic Press. p 504-538.

Appendix A

Vegetation Types in Sénégal (from Frederiksen and Lawesson, 1992)

Sahelian Grassland

1. *Calotropis procera – Balanites aegyptiaca*
2. *Acacia Senegal – Balanites aegyptiaca*

Semi-desert grassland

3. *Boscia senegalensis - Balanites aegyptiaca - Calotropis procera*

Sahelian wooded grassland

4. *Guiera senegalensis*

Sudanian woodland

5. *Pterocarpus lucens*
6. *Combretum glutinosum - Guiera senegalensis*

Sudanian woodland

7. *Strychnos spinosa – Sterculia setigera*
8. *Acacia macrostachya – Celtis intergrifolia*
9. *Bombax costatum – Maytenus senegalensis*

Sudano-Guinean woodland – grassland mosaic

10. *Acacia dudgeoni*
11. *Mitraguna inermis – Anogeissus leiocarpus*
12. Dry forest

Sudano-Guinean woodland and forest

13. *Prospis Africana – Pterocarpus erinaceus*
14. *Daniella oliveri – Annona senegalensis*
15. *Combretum nigracans*
16. *Erythrophleum suaveolens – Dialium guineense*